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The lucinid bivalve genus *Cardiolucina* (Mollusca, Bivalvia, Lucinidae): systematics, anatomy and relationships

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SYNOPSIS. The marine lucinid genus *Cardiolucina* (usually known as *Bellucina*) comprises 11 living species of small, heavily ornamented, subspheroidal bivalves. The type species of the genus is the Miocene fossil *C. agassizi* (Michelotti). A new definition and description of the genus is given. All the living species and the type species are redescribed and illustrated. Two species, *C. australopilula* from Western Australia and *C. siquijorensis* from the Philippines, are described as new. Anatomical details are given for two species which both contain chemosymbiotic bacteria in the ctenidia. A preliminary phylogenetic analysis using shell characters and *Parvilucina* as an outgroup, indicates three clades of *Cardiolucina*. Nine species are found in the Indo-W. Pacific and two in the tropical Atlantic. The greatest diversity occurs around Australia where seven species live. The two Atlantic species are similar to the widespread Indo-Pacific species *C. semperiana*. The earliest-known species of *Cardiolucina* is from the Eocene, but the fossil record is very poor.

INTRODUCTION

Since the discovery of endosymbiotic sulphur-oxidising bacteria contained in the gills, the biology of bivalves in the family Lucinidae has attracted much attention (Fisher & Hand, 1984; Dando, Southward, Southward, Terwilliger & Terwilliger, 1985; Dando, Southward & Southward, 1986: Southward, 1986; Reid & Brand, 1986; Distel and Felbeck, 1987; Cary, Vetter & Felbeck, 1989; Fisher, 1990; Reid, 1990). The symbiosis has so far been recorded in about 25 species of Lucinidae and some species have been shown to be nutritionally dependent on the association (Le Pennec, Beninger & Herry, 1995). The discovery and investigation of the symbiosis has been the key to understanding the many unusual features of lucinoid morphology and habitat distribution (Allen, 1958; Reid & Brand, 1986, Reid, 1990). Despite the burgeoning biological interest in lucinid bivalves, it is unfortunate that the systematics of family are not well understood, with many taxonomic groups, particularly at the supraspecific level, being rather loosely defined. Most recent comprehensive systematic treatments of Lucinidae (Chavan, 1969; Bretsky, 1976) both predate the discovery of chemoautotrophy in the family and, moreover, are based entirely on shell characters. As Hickman (1994) points out, there has been no attempt to incorporate the potential wealth of anatomical and biological characters into systematic studies. Furthermore, following closer attention to lucinid biology and the investigation of new habitats it is now being recognised that there are many undescribed species.

In this paper, we review the species of the lucinid genus *Cardiolucina* (better known as *Bellucina*), which are largely tropical, small, subspheroidal bivalves found in the Indo-Pacific and Atlantic Oceans. The impetus for this revision stems from the discovery of two coexisting lucinids in the shallow waters around the Abrolhos Islands, Western Australia (Glover & Taylor, 1997). Both species appeared to be undescribed and one with unusual periostracal extensions has been assigned to a new genus *Rastafaria* (Taylor & Glover, 1997). The other species, which forms a part of this paper, was evidently a *Cardiolucina* and seemed similar to *C. semperiana* Issel, which is widespread in the Indo-West Pacific. However, preliminary research indicated that there is much taxonomic confusion within the genus, including the priority of the name *Cardiolucina* over *Bellucina*. This led us to revise and redescribe the type species, provide a new diagnosis of the genus, to review the Recent species from the Indo-Pacific and Atlantic Oceans and to describe new species from Western Australia and the Philippines. We have also attempted to identify within the genus *Cardiolucina* those shell and anatomical characters that might be used in a wider study of lucinid systematics.

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ABBREVIATIONS

Institutions: AM – The Australian Museum, Sydney; ANSP – Academy of Natural Sciences, Philadelphia; BMNH – The Natural History Museum, London; MNHN – Muséum National d'Histoire Naturelle, Paris; IRSNB – Royal Belgian Institute of Natural Sciences; NM – Natal Museum; NMW – National Museum of Wales, Cardiff; NSMT – National Science Museum, Tokyo; SAM – South Australian Museum, Adelaide; USNM – National Museum of Natural History, Washington; UMT – University Museum, Tokyo; WAM – Western Australian Museum, Perth; ZMA – Zoological Museum, Amsterdam; ZMC – Zoological Museum, Copenhagen.

Shell measurements: H= height of shell from umbone to ventral margin, L = length of shell from anterior to posterior, T= tumidity of shell i.e. maximum convexity measured on a single valve.

SYSTEMATIC DESCRIPTIONS

Family **LUCINIDAE** Fleming, 1828
Genus ***CARDIOLUCINA*** Sacco, 1901

Cardiolucina Sacco, 1901: 89. Published June 30 (see Sacco, 1904; Marshall, 1991).

Bellucina Dall, 1901: 806. Published August 22nd (see Keen, 1971: 983). *Lucina eucosmia* Dall, 1901: 806, original designation.

TYPE SPECIES. *Cardium agassizi* Michelotti, 1839 (original designation).

NOMENCLATURE. The species considered in this paper have usually been assigned to the genus *Bellucina* Dall, 1901. However, the Miocene *C. agassizi* Michelotti, the type species of the genus *Cardiolucina* Sacco 1901, has all the characters of Recent *Bellucina* species (see description and figures of *C. agassizi* below). Chavan (1937) recognised this and synonymized the two genera giving *Bellucina* priority. Although published in the same year, Sacco's work appeared in June 1901 (Sacco, 1904, Marshall, 1991) and Dall's in August (see Keen, 1971). *Cardiolucina* therefore has priority over *Bellucina*.

Because the name *Bellucina* has been commonly used, the concept of this genus has to be considered in some detail. Dall (1901, p. 806) erected *Bellucina* as a section of the subgenus *Parvilucina* within the genus *Phacoides*. The genus *Parvilucina* was originally diagnosed as 'Shell small, plump, often inequilateral; sculpture more or less reticulate but not muricate, teeth small, common but all usually present' and the Section *Bellucina* was rather skimpily distinguished as 'Dorsal areas and sculpture strong.' However, Dall (1901) clearly designated *Lucina eucosmia* (= *L. pisum* Reeve) as the type species and the concept of *Bellucina* must be based upon this species. Many authors (e.g. Fischer, 1871, Lamy, 1920; Chavan, 1969; Britton 1972; Bretsky, 1976; Oliver, 1992) have considered *B. eucosmia* to be synonymous with *Bellucina semperiana* (Issel, 1869). Consequently, the characters of the latter species have been taken to represent *Bellucina*. Unfortunately, Reeve (1850) mixed two distinct species in the original description and illustrations of *Lucina pisum* which is clear from the syntype material. Reeve's figure 66a illustrates a specimen from Port Essington, Northern Territory, Australia, and figure 66b shows a shell of another species from Singapore. In the original description of *Lucina pisum* Reeve clearly referred to the deeply incised lunule and fenestrate ornament which are features of the Port Essington specimens. '*Shell globosely cordate, solid, thickly latticed with concentric and radiating ribs, of which the interstices are pitted, posterior side grooved, anterior short, lunule small, deeply excavated; whitish.*' For this reason one of the syntypes from Port Essington has been selected as the lectotype of *Lucina pisum* Reeve (see below under description of *Cardiolucina eucosmia*). Because the name *L. pisum* is preoccupied (*L. pisum* Sowerby, 1836) then *C. eucosmia* (Dall, 1901) becomes the valid replacement name. The other Reeve syntypes from Singapore we consider to be *Cardiolucina semperiana* (see below).

DIAGNOSIS. Shells small but solid, usually less than 14mm in height, subcircular (Height/Length ratio around 1.0), moderately inflated to subspheroidal (Tumidity/Length ratio between 0.38 and 0.48). Umbones prosogyrate, more or less central. Anterior sulcus either absent or shallow and narrow. Posterior sulcus always present and either deeply-indented or shallow. Lunule varies in size and depth between species, but where visible it is generally heart shaped. It can be deeply incised and large as in *C. eucosmia*, or very small and hidden under the beaks as in *C. australopilula*. Posterior dorsal area distinct, either concave or convex, usually with concentric ribbing. Ornament of radial ribs and concentric lamellae, relative strength of either varies between species. Concentric lamellae often raised and fluted. Intersection with radial ribs produces a variety of ornament from fenestrate to beaded. Hinge plate thick, dentition of single anterior and posterior lateral and two cardinal teethin each valve. In the right valve of some species one of the cardinal teeth can be either reduced or absent. Ligament external and varying in length; can extend from beaks to position of posterior lateral tooth, or may be two thirds of this distance. Internal ventral margin finely to coarsely crenulate, corresponding to position of radial ribs. Often small denticles around antero- and postero-dorsal margins. Anterior adductor muscle scar quadrate to elongate, ventral tip only slightly detached from pallial line. Mature individuals of spheroidal species often have the adductor muscle scars located on an internal buttress. Posterior adductor scar short and rounded.

Juvenile shells are thinner, less inflated, more anteriorly extended with radial ribs often visible from interior of shell. Interior ventral margin not thickened.

ANATOMY. Based on observations of *C. australopilula* and *C. semperiana*.

Mantle largely unfused except at posterior exhalant aperture. Mantle margin thick and muscular. Mantle 'gills' absent. No fused inhalant aperture. Exhalant aperture a muscular tube with flared distal end, which can presumably be protracted. Ctenidia consist of inner demibranchs only, filaments elongate and thick. Outer lamella of demibranchs attached to posterior mantle just ventral to the exhalent aperture. Labial palps are small ridges at edge of lips. Foot cylindrical and vermiform with a posterior heel. Body wall muscular, with large hemispherical visceral pouch containing oocytes. Rectum curves around dorsal side of the posterior adductor muscle and opens near the posterior aperture.

Many of the anatomical features, such as the thickened inner demibranchs, reduced labial palps and vermiform foot are similar to those of other lucinids, although some characters may be less widely distributed. A distinctive and possibly functionally important feature is the attachment of the ctenidia to the posterior mantle. It is uncertain how widely this character is distributed amongst the Lucinidae. It was first illustrated by Reid & Brand (1986) for *Parvilucina tenuisculpta*, but not mentioned by Allen (1958) in his general survey of lucinoids, or by Morton (1979) for *Fimbria* and not present in *Rastafaria* (Taylor & Glover, 1997). Large hemispherical visceral lobes or pouches are not present in most Lucinidae (Allen, 1958), but are found in *Parvilucina* (Reid & Brand, 1986), and species of Thyasiridae have several pouches (Allen, 1958). Most Lucinidae seem to possess both inhalant and exhalant posterior apertures, produced by mantle fusion (Allen, 1958). In *Cardiolucina* there is no inhalant aperture, a state found also in *Parvilucina* (Reid & Brand, 1986).

Cardiolucina species share three anatomical characters with *Parvilucina tenuisculpta*, namely; the attachment of the posterior ctenidia to the mantle, the hemispherical visceral pouches and the lack of inhalant apertures. These characters may indicate a possible relationship, but the distribution of most anatomical characters amongst the Lucinidae is not well known.

GEOLOGICAL RANGE. Eocene (Lutetian) to Recent.

COMPARISON WITH OTHER GENERA. There has been a tendency to place small, inflated lucinids with both radial and concentric ornament, rather arbitrarily into a number of genera such as *Phacoides*, *Parvilucina*, *Linga* and *Bellucina*. These decisions have usually been made without reference to the characters of the type species. For instance, the status of *Bellucina* in major taxonomic revisions has varied as follows:

Phacoides (Parvilucina) section *Bellucina* – Dall, 1901: 806
Phacoides (Bellucina) – Lamy, 1920: 211
Linga (Bellucina) – Chavan, 1937: 205; 1969: 496
Parvilucina (Bellucina) – Britton, 1972: 15
Lucina (Bellucina) – Bretsky, 1976: 272–3

Cardiolucina (as *Bellucina*) has often been considered as a subgenus of *Parvilucina* Dall, 1901, type species *Lucina tenuisculpta* Carpenter, 1864, which ranges from Alaska to Baja California. Hickman (1994) redescribed and illustrated *P. tenuisculpta* and two other west American species. Although they are small, rounded and fairly inflated, *Parvilucina* species are thinner shelled and less tumid (T/L 0.29) than all *Cardiolucina* (T/L 0.38–48) species. Most *Cardiolucina* have a pronounced posterior sulcus, and sometimes a narrow anterior sulcus, compared to the weak, shallow, posterior sulcus of *Parvilucina*. *Parvilucina* has both radial and concentric ribs; the radial ribbing consisting of closely-spaced, low riblets, which are generally weak, but most prominent at the anterior and posterior of the shell. The internal ventral margin of *Parvilucina* is finely denticulate, compared with the coarser crenulations of *Cardiolucina*. The lunule in *Parvilucina* is narrowly lanceolate and asymmetric with the right valve overlapping the left, compared with the shorter, heart-shaped lunule of *Cardiolucina agassizi*. The hinge plate of *Parvilucina* is also thinner and the lateral teeth distant from the cardinals. Although a major reappraisal of the relationships of these genera is necessary, evidence suggests that the *Parvilucina* taxa centred around the type species, represent a clade distinct from *Cardiolucina*.

Another genus which should be considered in relation to *Cardiolucina* is *Radiolucina* Britton, 1972, (type species *Phacoides amiantus* Dall, 1901) from the Caribbean. Dall placed this species and the similar West American species *L. cancellaris* Philippi, 1846 in *Bellucina*. Later, Keen (1971, p.121) recognised that they were only superficially similar to the type species of *Bellucina* and placed them in the subgenus *Pleurolucina* Dall, 1901, remarking that American authors had been slow to recognise Dall's error. Bretsky (1976) confusingly gave an extensive diagnosis of the genus *Bellucina* based on *P. amiantus* rather than the type species *Bellucina eucosmia*. Britton (1972) had previously compared *P. amiantus* with *Bellucina semperiana* (Issel) which he considered the type species of *Bellucina* and recognised that *P. amiantus* represents a distinct and separate lineage within the Lucinidae. For this reason, he erected a new subgenus *Radiolucina*. The type species, *R. amianta* has a more elongate shell than most *Bellucina* species H/L 0.92 (data from Bretsky, 1976, p. 273) compared with about 1.0 for *Cardiolucina* species, and the shell is less tumid T/L 0.33 compared with 0.43 for *Cardiolucina*. Furthermore, *R. amianta* has 8–12 broad radial ribs crossed by threadlike concentric lamellae, often with intermediate secondary radial ribs in the ventral two thirds of the shell. We agree with Keen (1971) and Britton (1972) that *Radiolucina amiantua* belongs to a distinct and separate clade which includes several fossil species from the south western USA. Therefore, Bretsky's (1976, p. 272) diagnosis of *Bellucina* based on *P. amiantus* should be rejected.

Some American palaeontologists (Woodring, 1925; Gardner, 1926) used the generic name *Cardiolucina* for some Miocene lucinids with high beaks and lacking radial ribs. These species are now placed in the genus *Cavilinga* Chavan, 1937 (see Olsson & Harbison, 1953 p. 85; Bretsky, 1976 p. 265).

Chavan (1937, 1969) classified *Bellucina* as a subgenus of *Linga* de Gregorio 1885, for which the type species is *Lucina columbella* Lamarck, 1818, a Miocene fossil from France. This is a large, very thick-shelled species with concentric ribs only and a strong posterior sulcus unlike *Cardiolucina*.

SPECIES DESCRIPTIONS

Cardiolucina agassizi (Michelotti, 1839)

Fig. 1

Cardium agassizi Michelotti, 1839: 17.
Lucina agassizi – Michelotti, 1847: 404 pl. 4 figs 4,5, 7.
Lucina irregularis Eichwald, 1853: 82–83, pl. 5 fig. 4.
Cardiolucina agassizi (Michelotti) – Sacco, 1901: 89–90, pl. 10 figs 37–39.
Phacoides (Cardiolucina) agassizi (Michelotti) – Cossmann & Peyrot, 1911: 688–689, pl. 28. figs 83–86.

TYPE MATERIAL. ?Museo di Paleontologia, Rome.

TYPE LOCALITY. Not given by Michelotti, but Sacco (1901) records several localities in the Miocene of Italy.

DESCRIPTION. Shell small, solid, height to 7.4 mm, subcircular, mean H/L 1.03, moderately inflated, mean T/L 0.39, tumidity to a maximum of 2.7 mm on a single valve. Shell inequilateral, extended anteriorly. Deep posterior sulcus with fine concentric lamellae. Shallow anterior sulcus. Lunule heart-shaped, small and shallow. Escutcheon lanceolate with concentric lamellae and a single strong radial ridge. Exterior sculpture of more than 25 faint, radial, rounded ribs with narrow interspaces. There are about 20 prominent, concentric lamellae which are often slightly recurved. Lamellae are extremely variable in thickness, degree of projection, recurvature and width of interspaces. Hinge plate thick. Left valve with single posterior lateral tooth, two cardinal teeth and single anterior lateral. Right valve with single posterior and anterior laterals and single cardinal. Ligament extending two thirds of the distance from umbone to posterior lateral tooth. Inner margin with 28–30 crenulations and small denticles along anterodorsal and posterodorsal margin. Anterior adductor muscle scar elongate, not buttressed, with pallial line attached near to the ventral tip. Posterior muscle scar ovate. Pallial line indistinct. Shell white.

In the material examined from France we found the concentric ornament to be extremely variable from separated, thin lamellae to clusters of thicker lamellae producing a rugose ornament (see Fig.

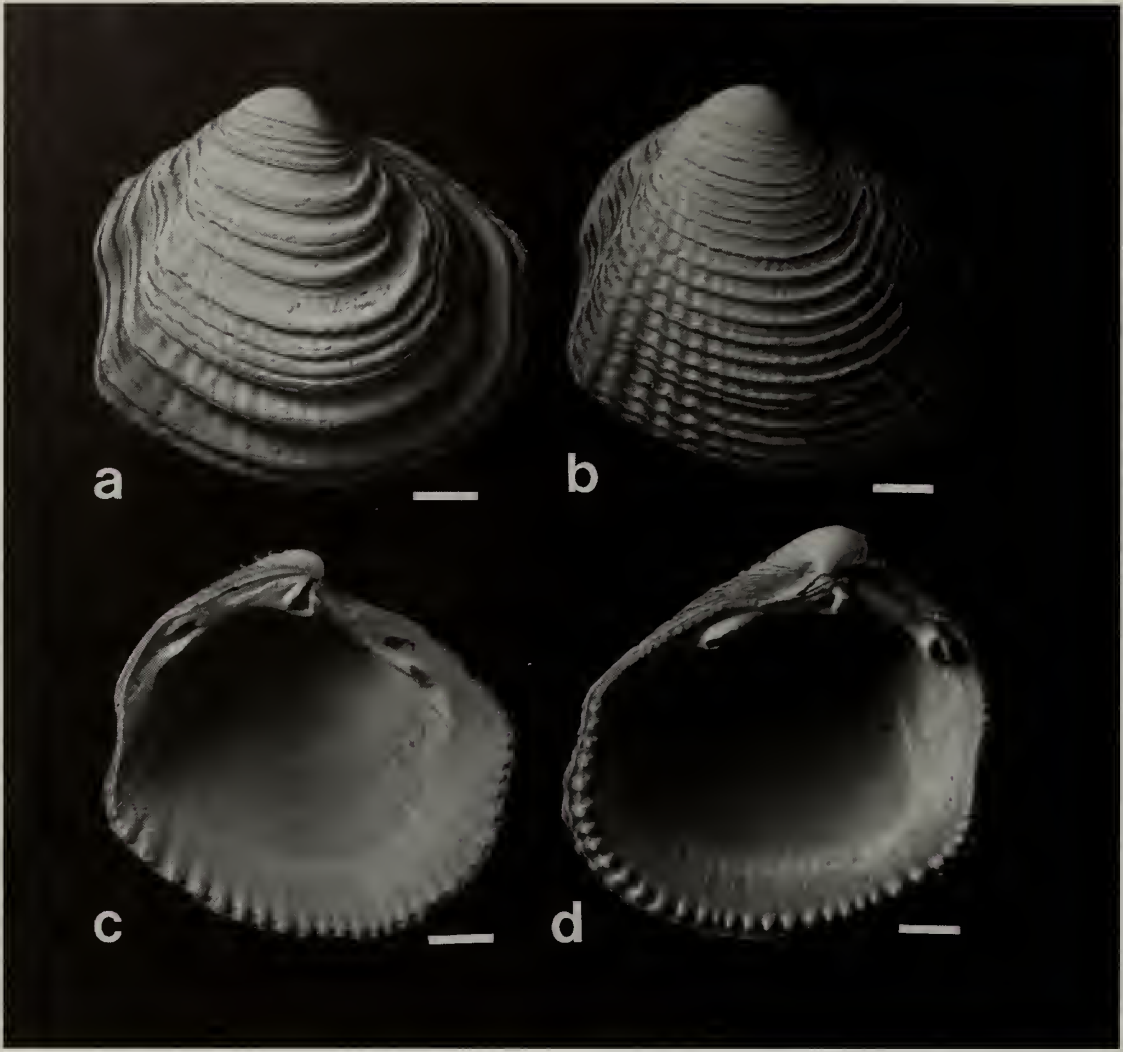

Fig. 1 *Cardiolucina agassizi* (Michelotti, 1839), middle Miocene (Langhian), St Jean de Marsacq, Landes, France. (coll Lozouet and Maestrati, MNHN) a, exterior of right valve; b, exterior of right valve; c, interior of left valve; d, interior of right valve. Scale bars a = 750μm, b =700μm, c = 1.5mm, d = 500μm.

1d). Similar variability of the concentric sculpture is seen in the Recent species *C. crassilirata* and *C. semperiana.*

DISTRIBUTION. As well as the records of Sacco (1901), *C. agassizi* is also recorded from the Tortonian of the Aquitaine Basin (Cossmann & Peyrot, 1911) and from the middle Miocene Korytnica Formation of Poland (Friedberg, 1934).

MATERIAL EXAMINED. **FRANCE**: Middle Miocene (Langhian), St Jean de Marsacq, Landes, France; ca 100 shells, Lozouet & Maestrati coll (MNHN).

Cardiolucina australopilula Taylor and Glover, new species

Figs 2–6

TYPE MATERIAL. Holotype: WAM reg number 110–96: H. 13.6, L. 12.8, T. 6.6 mm. Paratypes: WAM 111–96 2 preserved specimens station 35; AM C.202975 1 preserved specimen, station 23; BMNH 1996086, 1996087, 1996088, 1996089 4 preserved specimens, stations 1, 33, 36, 37; BMNH 1996090 one dry shell station 36. (Station data in Glover & Taylor, 1997).

TYPE LOCALITY. 9 km north of Beacon Island, Wallabi Group, Houtman Abrolhos Islands, Western Australia, 113° 46'E, 28° 23'S, depth 39m.

SHELL DESCRIPTION. Shell solid, small, height to 13.8 mm, subcircular in outline, H/L mean 1.03, inflated, orbicular, T/L mean 0.47, tumidity to a maximum of 7.5 mm on a single valve. Shell slightly inequilateral, extended anteriorly. Very shallow posterior sulcus. Umbones pronounced, prosogyrate. Lunule extremely small and shallow. Anterodorsal area slightly convex, heart-shaped in outline and with fine concentric ribbing. Escutcheon broadly lanceolate, convex and finely ribbed with concentric and a few radial ribs. Exterior sculpture of about 20 radial ribs, rounded in profile, separated by flat interspaces. Anteriorly, interspaces are as wide as the ribs, elsewhere interspaces are about two thirds of the width of radial ribs. Radial ribs have very fine radial striations (Fig. 3d). Radial ribs are crossed by 34–36 thin, low, concentric lamellae and their intersection produces a finely fenestrate ornamentation. Hinge plate thick, left valve with single posterior lateral tooth, two cardinal teeth, the anterior of these is robust and hooked (Fig. 3c) and a single anterior lateral. Right valve with single posterior lateral

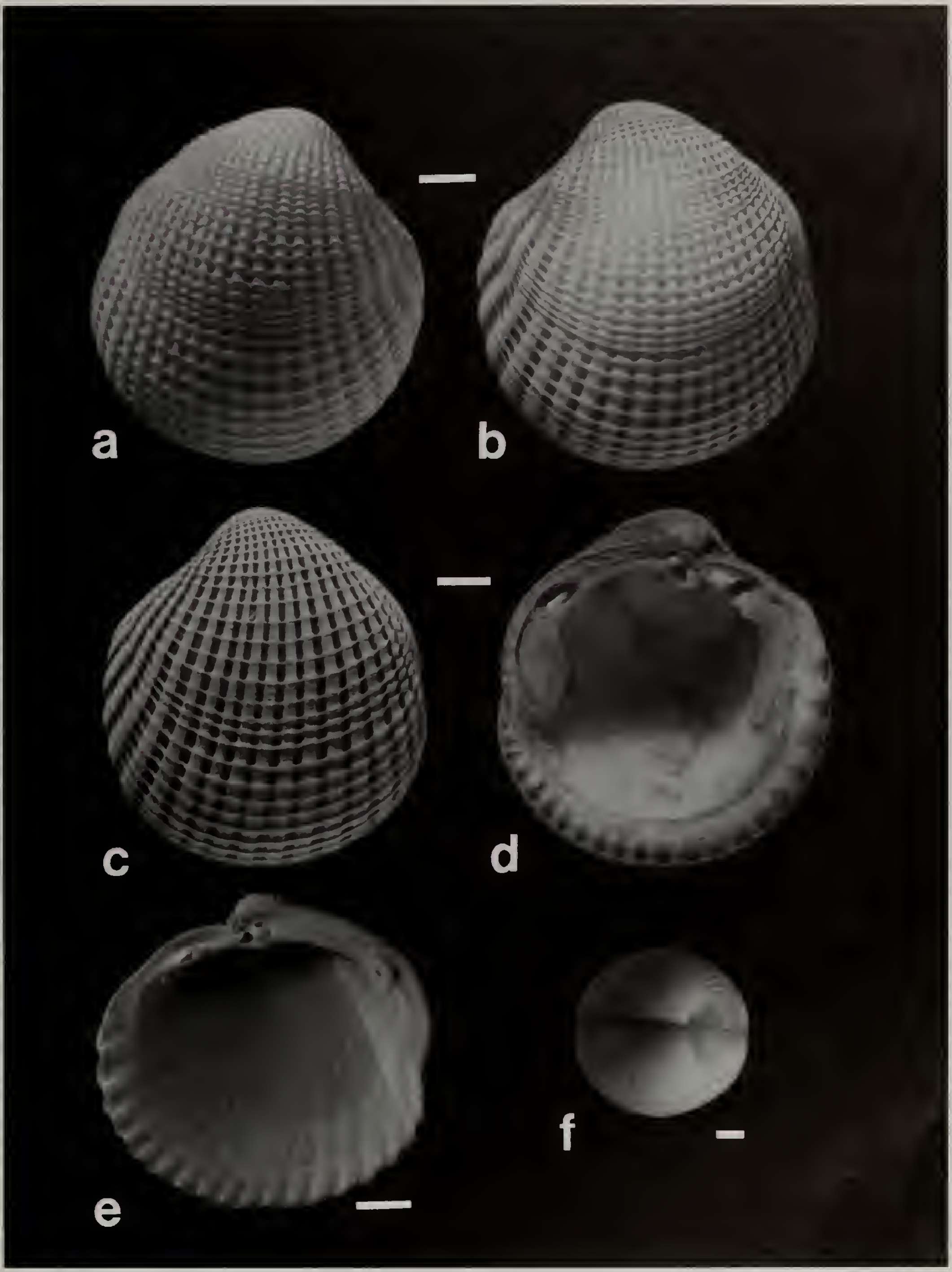

Fig. 2 *Cardiolucina australopilula* Taylor and Glover new species, Beacon Island, Wallabi Group, Houtman Abrolhos Islands, Western Australia. a, Holotype (WAM 110–96), exterior of right valve; b, Holotype, exterior of left valve; c, Paratype (BMNH 1996090), exterior of left valve; d, Paratype (BMNH 1996090), interior of left valve; e. interior of right valve of juvenile shell, Eagle Bluff, Peron Point, Shark Bay; f, Holotype dorsal area. Scale bars a–d = 2.0mm, e = 2.5mm, f = 2.0mm.

tooth, two cardinal teeth, the posterior larger than the anterior, and a single anterolateral. Cardinal teeth sit on a curved, ventrally projecting buttress. Ligament elongate, extending from beak to posterior lateral tooth. Inner margin of shell thickened with 21 crenulations. Small sinus on posterolateral margin corresponding to the position of the posterior sulcus. Anterior adductor muscle scar narrow, elongate and sited on a buttress with ventral third detached from the pallial line. Posterior muscle scar ovate. Pallial line continuous. Shell colour white.

Juvenile shells (Fig 2e) less inflated, more anteriorly extended. External radial ribs visible on interior of shell.

ANATOMY. The mantle margin is thick and fused only at the posterior exhalant aperture (Fig. 4), and there is no fused inhalant

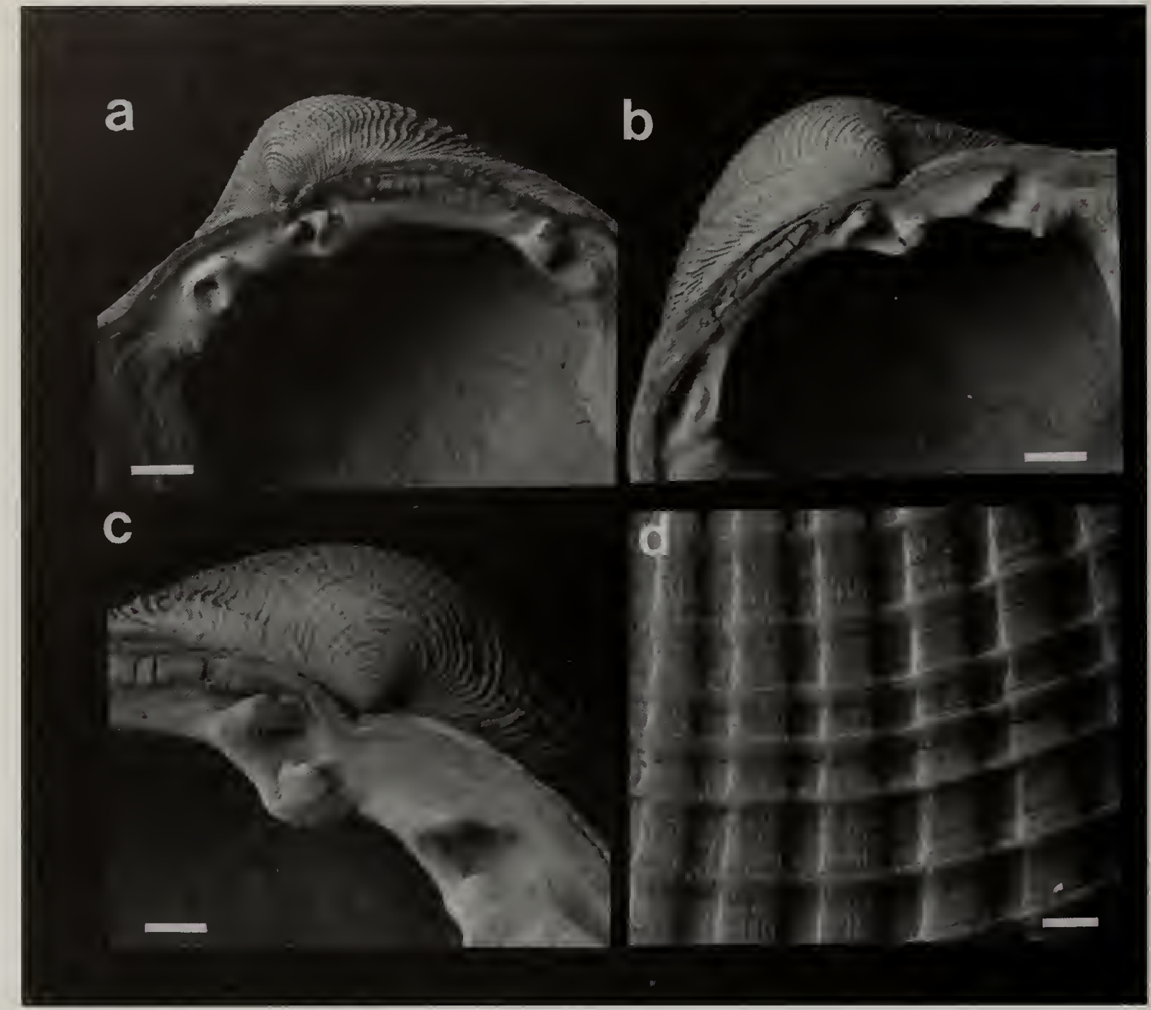

Fig. 3 *Cardiolucina australopilula* new species. a, Holotype, hinge in the right valve; b. Holotype, hinge in the left valve; c, Paratype, left valve, detail of cardinal teeth; d, outer shell surface showing radial striations on radial ribs. Scale bars a=2.0mm, b=2.5mm, c=1.0mm, d=500µm.

aperture. The exhalant aperture consists of a muscular tube with a flared distal end, which is inverted in preserved specimens, but can presumably be protracted. The ctenidia comprise inner demibranchs only. These have large, thick filaments which are fused between the ascending and descending lamellae. To the posterior, the outer lamellae are attached to the mantle margin just ventral to the exhalant aperture. The attachment area forms a thin, muscular septum. The labial palps consist of small folds at the edge of the thin, ridge-like lips. The foot is cylindrical and vermiform, tapering to a blunt point and extending posteriorly with a rounded heel. The visceral mass is covered by a muscular wall with a single, large, hemispherical visceral lobe on each side. The rectum runs around the dorsal side of the posterior adductor muscle and opens into the mantle cavity close to the exhalant tube.

COMPARISON WITH OTHER SPECIES. This species is similar in size, shape and sculpture to *C. quadrata* (Prashad, 1932) (Fig. 16) but differs in the greater prominence of the radial ribs and thinner, concentric lamellae. *C. australopilula* is also more tumid and spherical. This species has been referred to as *Bellucina* cf. *semperiana* by Slack-Smith (1990), but *semperiana* is smaller, with different ornamentation and hinge teeth.

HABITAT. Fine, well-sorted, calcareous sand between 30–40m, in association with other bivalves *Amusium balloti, Mimachlamys australis* and *Rastafaria thiophila* (Glover & Taylor 1997).

DISTRIBUTION. Western Australia, Houtman Abrolhos Islands to Broome (Fig. 6).

ETYMOLOGY. *australopilula* meaning 'Australian little ball'.

MATERIAL EXAMINED. **WESTERN AUSTRALIA**: Broome (AM C.309449); Roebuck Bay, Broome (BMNH 1892.1.29.121); Montebello Islands, Bunsen Channel, N. end of Trimoville I. 20° 23.8'S; 115° 32.43'E 3m (WAM); Barrow Island 20° 53'S, 115° 20'E (WAM); Exmouth Gulf (WAM 3461–3468); Mauds Landing, N.W. Cape, 3m (WAM); Turtle Beach, off N.W. Cape (AM C.309456); Carnarvon (AM C.309455); Dirk Hartog Island, 10–20m (WAM 3475.68); Bernier Islands 24° 53.3'S 113° 17.5'E. (WAM); Shark Bay, Peron Peninsula (WAM 249.94); Shark Bay, 5 km E.S.E. Cape Heirisson, 18m (WAM); Shark Bay, Freycinet Estuary (WAM 252–94). Houtman Abrolhos Islands: N. of Wallabi Islands, 40m (BMNH acc 2384); Easter Group, 50m (WAM N–2777); Zeewyk Channel, 40m (WAM N–2822); Little North Island, Easter Group, 40m (WAM); Rat Island, 30m (WAM wet material); East of Good Friday Bay, 28° 39.5'S – 113° 49.5'E, 40m (WAM).

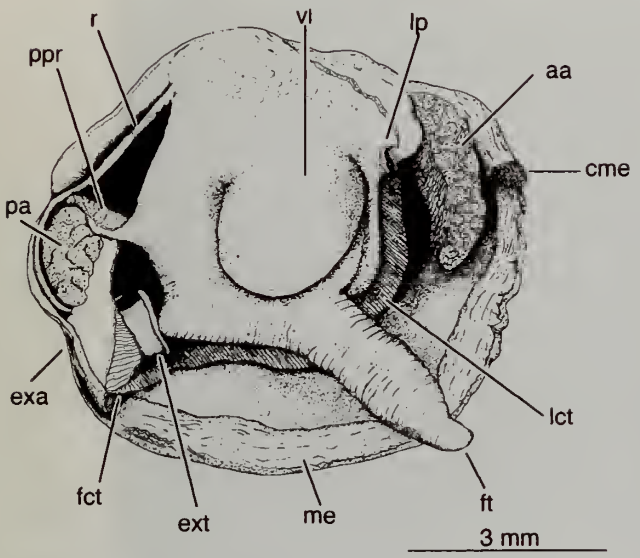

Fig. 4 *Cardiolucina australopilula* anatomy. Right mantle and ctenidium removed. Abbreviations aa – anterior adductor muscle, cme – cut mantle edge, exa – exhalant aperture, ext – exhalant tube, fct – fused ctenidium to mantle, ft – foot, lct – left ctenidium, lp – labial palps, me – mantle edge, pa – posterior adductor muscle, ppr – posterior pedal retractor muscle, r – rectum, vl – visceral lobe.

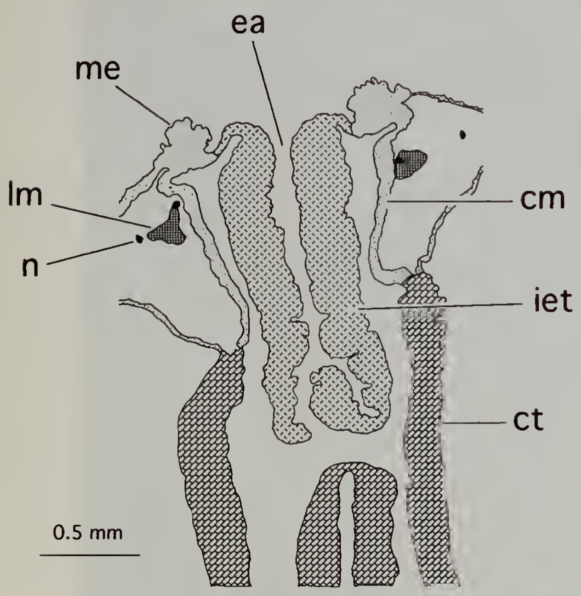

Fig. 5 Semidiagrammatic transverse section through the posterior exhalant area of *C. australopilula* showing the inverted exhalant tube and the connection of the ctenidium to the mantle. Abbreviations: cm – connection between mantle and ctenidium, ct – ctenidium, ea – exhalant aperture, iet – inverted exhalant tube, lm – longitudinal muscle, me – mantle edge, n – nerve.

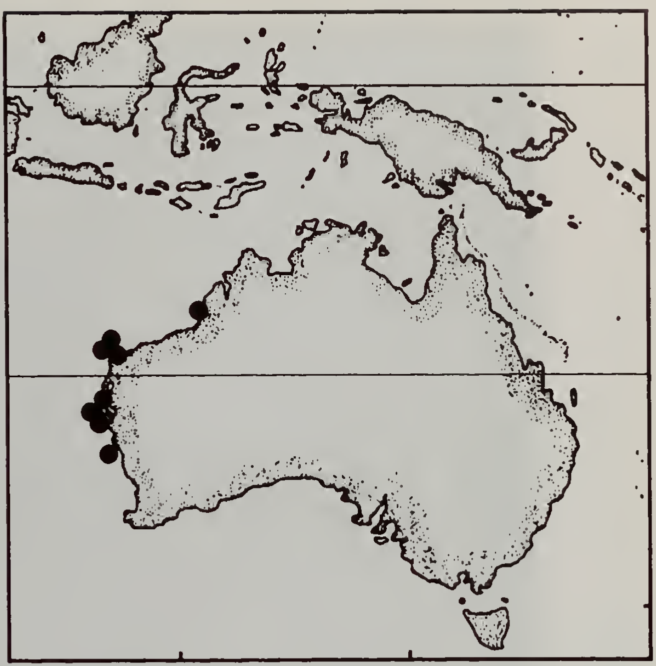

Fig. 6 Geographical distribution of *Cardiolucina australopilula* new species.

Cardiolucina civica (Yokoyama, 1927)

Figs 7–9

Cardium civica Yokoyama, 1927: 179. pl. 48, figs 3 & 4.
Dentilucina (Bellucina) hedleyi Prashad, 1932: 163–164, pl. 5, figs 17 & 18.
Bellucina civica (Yokoyama, 1927) – Kuroda, Habe & Oyama, 1971: 394, pl. 118 figs 17 & 18.
Lucina (Codakia) semperiana (Issel, 1869) – Melvill & Sykes, 1898: pl. 3, fig.1.

TYPE MATERIAL. *C. civica* syntypes, University Museum, Tokyo, CM 24913–24914, see Makiyama (1959); *C. hedleyi* holotype, 1 individual 2 valves (ZMA).

TYPE LOCALTIES. *C. civica* was described as a Pliocene fossil from Nagaya and Kakuma in Kaga Province, Japan. *C. hedleyi* from the Philippines, Sulu Archipelago, Siboga station 105 (6° 8'N, 121° 19'E), depth 275 m.

NOMENCLATURE. We have examined the holotype of *C. hedleyi* from Indonesia, which is very similar to both Recent specimens of *C. civica* from Japan and the fossils figured by Yokoyama (1927) and consider them conspecific.

SHELL DESCRIPTION. Shell solid, small, height to a maximum of 10.6 mm; subcircular, mean H/L 1.02, inflated, mean T/L 0.40, tumidity to a maximum of 4.5 mm on a single valve. Shell slightly extended anteriorly. There is a shallow posterior sulcus which has concentric ribs. Lunule small and shallow. Anterodorsal area weakly defined. Escutcheon slightly convex and finely ribbed. Exterior sculpture of numerous (more than 30) fine, slightly rounded, radial ribs with narrow interspaces. Radial ribs are crossed by many (more than 25) conspicuous concentric lamellae, which are rounded in profile and slightly recurved. Left valve with a single posterior lateral, two cardinal teeth and a single posterior lateral; right valve with a single posterior lateral, two cardinal teeth, the posterior

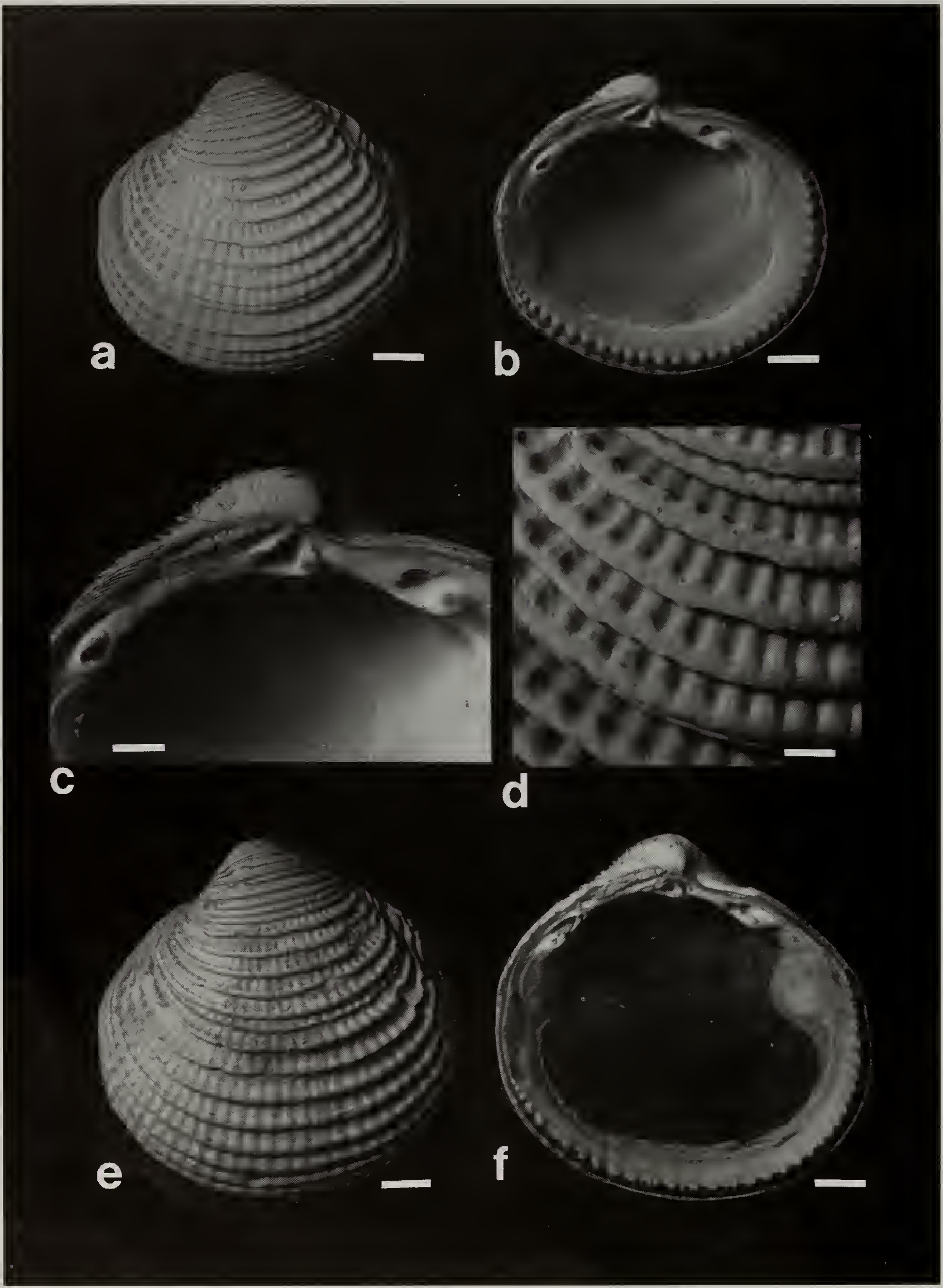

Fig. 7 a–d *Cardiolucina civica* (Yokoyama, 1927) southern Honshu, Japan BMNH 1878.10.16.191 and e–f *Dentilucina (Bellucina) hedleyi* Prashad, 1932 Holotype, Sulu Archipelago, Philippines. a, exterior of left valve; b, interior of left valve; c, hinge in left valve; d, outer surface of shell showing concentric and radial ribs; e, Holotype *C. hedleyi* exterior of left valve; f, Holotype *C. hedleyi* interior of left valve. Scale bars a=2.5mm, b=1.2mm, c=500µm, d=500µm, e=2.0mm, f=2.5mm.

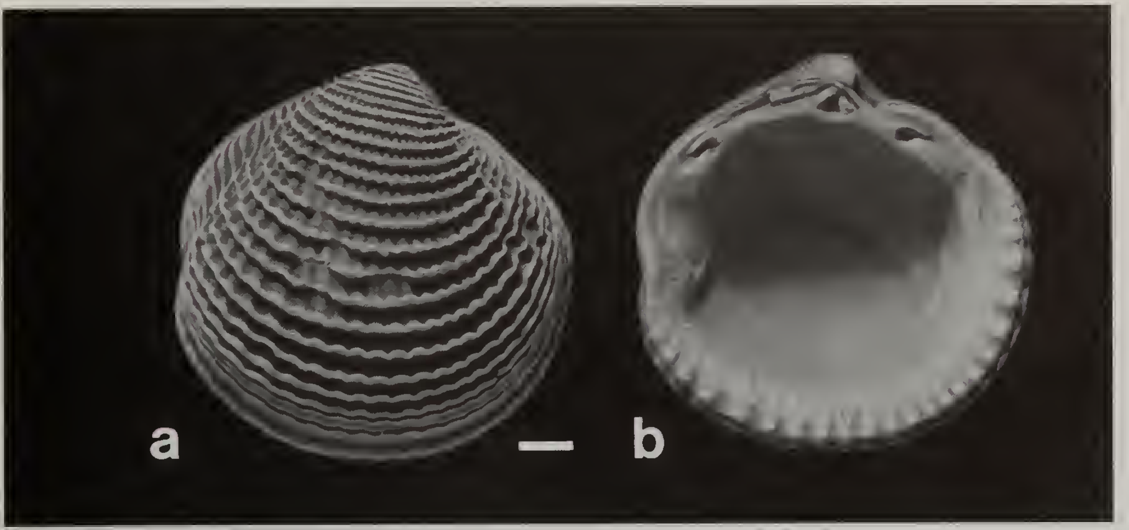

Fig. 8 *Cardiolucina civica* from Andaman Islands. Large specimen illustrated by Melvill and Sykes (1897, fig.1) as *Lucina (Codakia) semperiana* Issel (BMNH 1898.4.30.7) a, Right valve exterior; b, Left valve interior. Scale bar a–b = 1.0mm.

cardinal large and the anterior very small. There is a single anterior lateral tooth. Ligament short, extending from the beak to about half way to posterior lateral tooth. Inner margin of shell thickened and with 30 crenulations. Small denticles on anterodorsal margin. Anterior adductor muscle scar elongate and not buttressed, pallial line attached near ventral tip. Posterior adductor scar small and rounded. Pallial line continuous. Shell grey white.

Juveniles less inflated and more extended anteriorly. Posterior sulcus more pronounced and anterodorsal shell margin markedly convex. Shell thinner with radial riblets visible from interior of shell.

A large specimen (BMNH 1898.4.30.7) from the Andaman Islands, figured by Melvill and Sykes (1898 pl.3, fig.1) as *Lucina (Codakia) semperiana*, has many of the characters of *C. civica,* although larger than specimens from other localities. Other specimens in the BMNH from Port Blair, Andamans are similarly large.

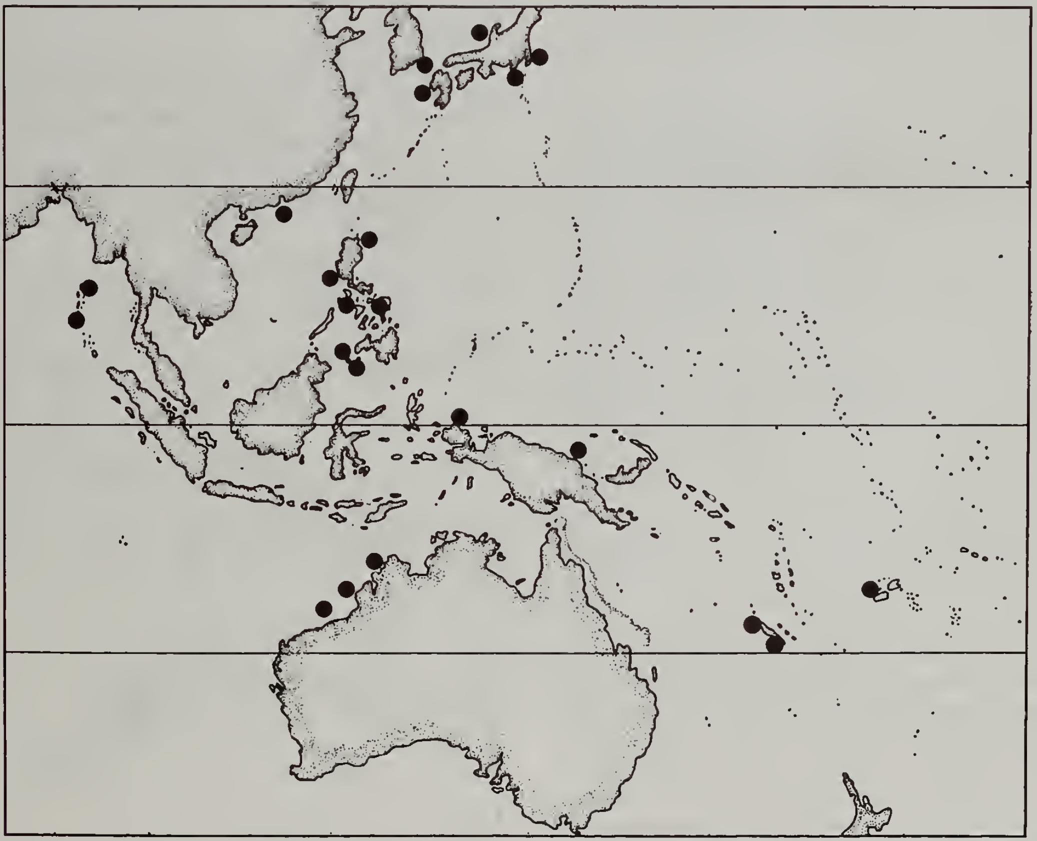

Fig. 9 Geographical distribution of *Cardiolucina civica* (Yokoyama).

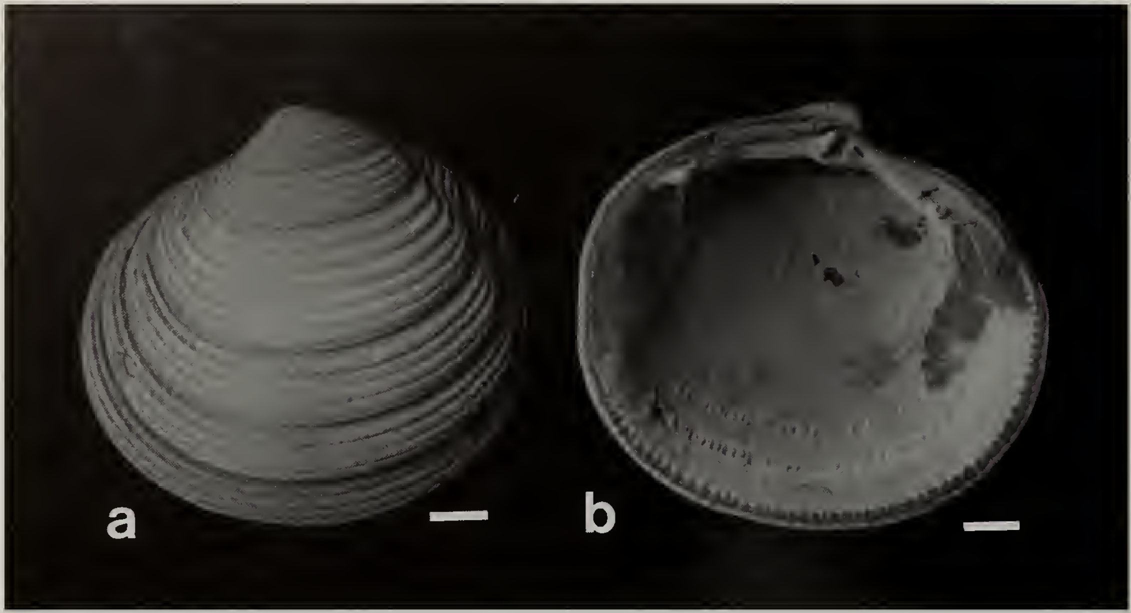

Fig. 10 *Cardiolucina crassilirata* (Tate, 1886), Western Port, Victoria, Australia. BMNH 1963200. a, exterior of left valve; b, interior of left valve. Scale bars a = 2.0mm, b = 2.5mm.

COMPARISON WITH OTHER SPECIES. *C. civica* is most similar to *C. crassilirata*, but it has a shorter ligament and coarser marginal crenulations.

HABITAT. Fine sandy and shelly bottoms mainly from shallow water to 200m, with a few dead shells recorded up to 600 m.

DISTRIBUTION. Andaman Islands, North Western Australia, South East Asia, Japan, to Fiji (Fig. 9).

MATERIAL EXAMINED. **ANDAMAN ISLANDS**: 11°37'N, 92°56'E, 357m (ANSP 292239); Port Blair, BMNH 1953.1.30.199–201; BMNH 1898.4.30.7. **AUSTRALIA**: Western Australia, N.W. of Port Hedland 19°13'S, 116°6'E, 271m & 19°24'S, 115°52'E, 238m (AM C.309458 & C.309453); N.W. Beagle Island, 29°43'S, 114°17'E, 274–283m (AM C.309465); N.W. Roebuck Bay, Broome 17°34'S 120°22'E, 188m (AM C.309457). **PHILIPPINES**: **Luzon**, off Matocot Pt W., 370m (USNM 295697); Tayabas Bay, off Tayabas Lt, 200m (USNM 297745); Ragay Gulf, off North Burias, 185m (USNM 246286); off Balanja Pt, S.E. Mindoro, 280m (USNM 295581); Adyagan I. E. Masbate,190m (USNM 298134); off Pt Dumurug, Masbate, 273m (USNM 298227); Linapacan Strait, 90m (USNM 301994); off Pt Lauis, E. Cebu, 280m (USNM 300493); off Gigantangan I., N.W. Leyte, 210m (USNM 298317); off Dammi I., Sulu Archipelago, 446m (USNM 299036); off Simaluc Island, Tawi Tawi Is, 600m (USNM 299195); off Jolo, Jolo I., 283m (USNM 294618) & 37m (USNM 294584); 14°01'N 120°18'E, 192m (MNHN). **CHINA**: off Pratas Islands., China Sea, 272m, (USNM 296724). **JAPAN**: off southern Honshu 34°13'N, 136°13'E, 90–100m (BMNH 1878.10.16.191); Kumano-Nada, off Kii Peninsula, 93m (NSMT 70534); off Jyogashima I., Miura Peninsula (NSMT 70535); off Goto Islands, 168m (NSMT 56297); off Tsushima Islands, 112m (NSMT 56298); Usibuka, Anakusa Island (NSMT 70533); Sagami Bay (USNM 708071). **IRIAN JAYA**: Aoeri I., Geelvink Bay, 1–40 (ANSP 275808, 280332); Japen I., Geelvink Bay, 30–40m (ANSP 277817, 276638, 279725); Schouten I., 18m (ANSP 280204). **NEW CALEDONIA**: 19°07'S 163°22'E, 110–200m (MNHN); 22°02'S 165°57'E 135–150m (MNHN); Grande Récif Sud, 22°42'S 157°22'E, 35m (MNHN). **FIJI**: Viti Levu Bay 0–5m near shore (USNM 878321).

Cardiolucina crassilirata (Tate, 1887)

Figs 10–11

Lucina crassilirata Tate, 1887a: 6–7, pl. 4 fig. 2.
Codokia crassilirata (Tate) – Cotton & Godfrey, 1938: 206 fig. 218.
Loripes crassilirata (Tate) – Pritchard & Gatliff, 1903: 139.
Bellucina crassilirata (Tate) – Macpherson & Gabriel, 1962: 327.

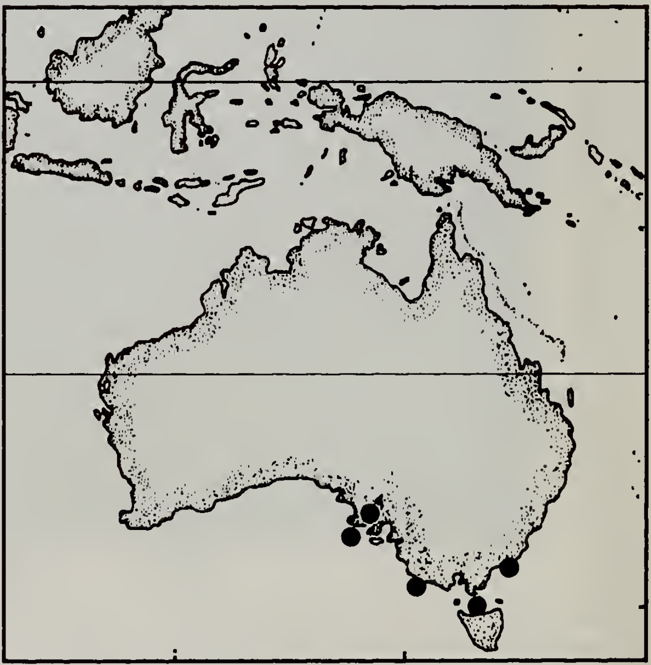

Fig. 11 Geographical distribution of *Cardiolucina crassilirata* (Tate).

Linga (Bellucina) crassilirata (Tate, 1887) – Lamprell & Whitehead, 1992: pl. 21 figs 128a & b.

HOLOTYPE. South Australian Museum No. D.12957. L = 8.5 mm, H = 8.3 mm, T = 7.0 mm.

TYPE LOCALITY. Streaky Bay, near Ceduna, South Australia.

SHELL DESCRIPTION. Shell small, solid, height to 8.4 mm, outline circular, H/L mean 0.98; shell moderately inflated with T/L mean 0.41, tumidity of a single valve to a maximum of 3.4 mm. Shell slightly inequilateral, extended anteriorly. Shallow sulcus posteriorly, with concentric lamellae. Lunule small and shallow. Escutcheon slightly convex, with fine concentric ribs. Exterior sculpture of more than 30 fine concentric lamellae, clustered in groups of 4–6 with broader interspaces between the clusters. Radial sculpture of many fine ribs visible in the interspaces of the concentric ribs. Hinge plate narrow; left valve with single posterior lateral, two cardinal teeth and single anterior lateral. Right valve with a single posterior and anterior laterals and two cardinal teeth, posterior cardinal larger than anterior cardinal tooth. Ligament long, extending from beaks to posterior lateral tooth. Inner margin with around 60 fine crenulations. Anterior adductor muscle scar, elongate, not buttressed, with ventral quarter detached from pallial line. Posterior adductor muscle scar ovate and not buttressed. Pallial line discontinuous. Shell greyish white.

COMPARISON WITH OTHER SPECIES. See *C. civica.*

HABITAT. Shallow subtidal to 70m.

DISTRIBUTION. South Australia, Victoria and Tasmania (Fig. 11).

MATERIAL EXAMINED. **AUSTRALIA**: **Victoria**, BMNH 1906.9.19.70–2; Western Port (BMNH 1963200); BMNH 1911.12.19.11–12; Western Port (WAM); Western Port (AM C.303440); Western Port, 15–18m (AM C.309469); Port Fairy, beach (ANSP 135488); **New South Wales**, Between Eagle and Crawfish Rock (AM); **South Australia**, Spencers Gulf (BMNH 1893.12.12.352–54); Hardwicke Bay (AM C.13463); Neptune I., 70m (AM); South Australia (AM C.6677); **Tasmania**, Geography Strait, 27m (AM C.38180).

Cardiolucina eucosmia (Dall, 1901)

Figs 12–13

Lucina pisum Reeve, 1850 (in part): pl. 11 fig. 66a (non *Lucina pisum* Sowerby,1836: 341).
Phacoides (Bellucina) eucosmia Dall, 1901: 806 (replacement name for *L. pisum* Reeve).
Phacoides eucosmia Dall. – Hedley, 1909: 426, pl. 37 fig 16.

TYPE MATERIAL. Lectotype here selected BMNH 1963194/1 (Figs 12a–d). Paralectotypes BMNH 1963194/2–3; 1845.825.210–212; 1963552 (this is *C. semperiana* see p. 107)

TYPE LOCALITY. Restricted to Port Essington, Northern Territory, Australia (modified from Reeve, 1850).

NOMENCLATURE. Many authors, for example Fischer (1871), Lamy (1920), Chavan (1969), Britton (1972), Bretsky (1976) and Oliver (1992) have considered *Lucina semperiana* Issel, 1869 a senior synonym of *P. eucosmia*. However, *Lucina pisum* Reeve, for which Dall gave the replacement name *Phacoides eucosmia*, is based on a syntype series composed of two distinct species. For the reasons given above in the generic section, we consider the specimens from Port Essington to conform most closely with Reeve's description and concept of *Lucina pisum* and one of these has been selected as a lectotype. The other syntypes from Singapore, now become paralectotypes and we consider these to be the eastern Indian Ocean form of *C. semperiana* (Fig. 21 a & b).

SHELL DESCRIPTION. Shell solid, small, height to 7.8 mm, subcircular in outline, slightly extended in an anterolateral direction, H/L mean 1.05; inflated, T/L mean 0.49, tumidity to a maximum of 3.8 mm on a single valve. Posteriorly, there is deep sulcus extending from hinge to ventral margin. The sulcus and the posterior portion of the shell has fine concentric ribbing with no radial ribs. The lunule is 'U'-shaped and deeply incised to the ventral edge of the hinge plate. Anterodorsal area is slightly convex, ovate in outline with fine concentric sculpture. Posterior dorsal area broadly lanceolate in outline, convex, with fine concentric ribbing. Exterior sculpture of about 12 broad, radial ribs with rounded profile, somewhat flattened on upper surface. Ribs narrower towards umbos. Interspaces between ribs deep, narrower than ribs. Radial ribs crossed by 13–14 thin, low, concentric lamellae which project slightly above radial ribs. The intersection of concentric and radial sculpture gives a distinctive fenestrate ornament. Hinge plate thick. Left valve has a single, strong lateral tooth posteriorly, two thin, cardinal teeth, the posterior tooth much larger than the anterior. Cardinal teeth are denticulate (see Fig. 12d). A single anterior lateral lies close to perimeter of the lunule. Right valve has a single posterior lateral, a large single cardinal tooth and a single anterior lateral. Both valves have small denticles around the dorsal margin of valve. Ligament elongate, extending from beak to posterior lateral tooth. Inner shell margin thickened, with 12 coarse crenulations. Small sinus on posterior lateral margin corresponding to position of sulcus. Anterior adductor muscle scar elongate, sitting on a shallow buttress with the only the ventral tip detached from the pallial line. Posterior adductor scar ovate on a shallow buttress. Pallial line is thin and continuous. Shell colour creamy white.

Juvenile shells (Figs 12 e & f) are less inflated and more extended anteriorly. The lunule is widely opened in younger stages. Denticles are absent on the dorsal inner margins. Radial ribs begin narrow and broaden ventrally between each concentric rib. Radial ribs are visible on interior of shells.

COMPARISON WITH OTHER SPECIES. Although *C. pisiformis, C. siquijorensis* and *C. australopilula* have a similar fenestrate ornament, *C. eucosmia* can be easily distinguished from all other species by the deeply incised lunule.

HABITAT. Low intertidal to 100 m in fine sand and mud. Hedley (1909) reports dredging the species in the Gulf of Carpentaria from about 10 m in soft black mud, where it was abundant.

DISTRIBUTION. Northern Australia (Fig. 13).

MATERIAL EXAMINED. **AUSTRALIA**: **Northern Territory and Queensland**, BMNH 1963490, 1963236, 1910.9.28.77–8; W. of Cape York, 8m (BMNH 1887.2.9.2776–7); Gulf of Carpentaria (NMW 1955.158); Sweers I. (AM C.75249, 78223); Forsyth I. (AM C.14892); Horsey River mouth, 9m (AM C.15152), Karumba (AM C.14963); Mapoon (AM C.14281); off Bountiful Islands (AM); Gulf of Carpentaria (AM C.100498); mid-Gulf of Carpentaria, 66m (AM); off Albany River (AM); Karumba Point (AM 1909); Albany Passage, 8–25m (AM C. 36172); Port Essington (BMNH; off Point Charles, Darwin, 27–37 m (AM C.309468); Van Diemen's Inlet (NMW 1955.158); Van Diemen's Inlet (AM C.15273); 100 miles N. of Croker Island, Arafura Sea, 124m (AM C.309454); 150 km N. of Coburg Peninsula, 108m (AM); Dinah Beach, Darwin (AM); Crocodile Research Station, Maningrida, Arnhem Land (AM);

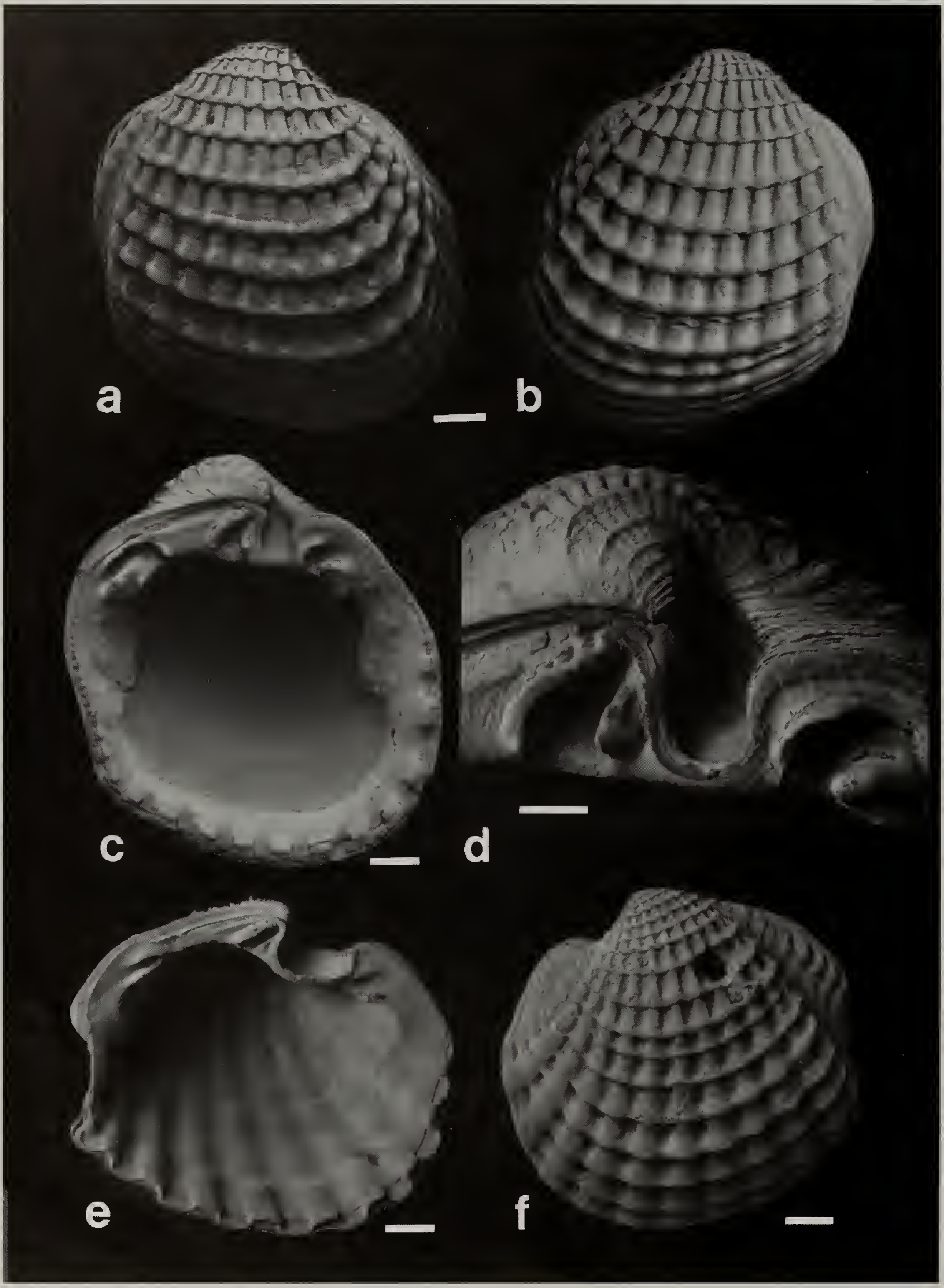

Fig. 12 *Cardiolucina eucosmia* (Dall, 1901) Port Essington, Northern Territory, Australia. Figured specimens a–d are the lectotype of *Lucina pisum* Reeve, BMNH 1963194/1. & Figure e–f *C. eucosmia*, Arafura Sea, Northern Territory, Australia, AM C.309454. a, exterior of right valve; b, exterior of left valve; c, interior of left valve; d, hinge and lunule in left valve; e, juvenile, interior of left valve; f, juvenile, exterior of left valve. Scale bars a–c = 1.0mm, d = 500μm, e = 650μm, f = 1.0mm.

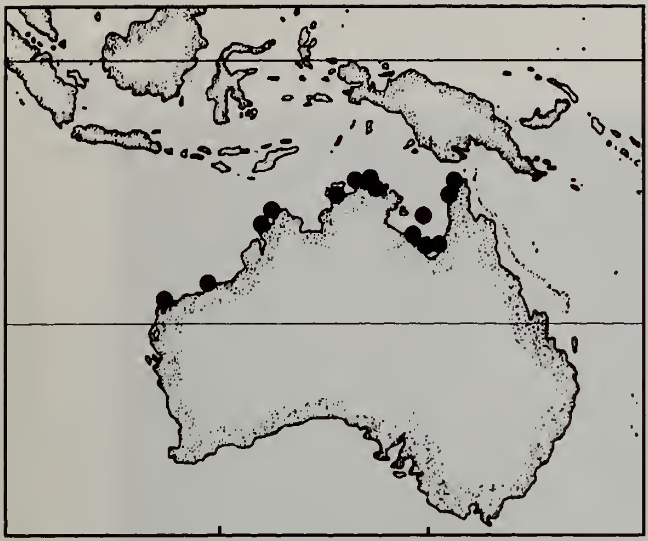

Fig. 13 Geographical distribution of *Cardiolucina eucosmia* (Dall).

Western Australia, Prince Frederick Harbour (WAM); Cape Leveque (AM); Port Hedland (AM); Direction Island, off Onslow (AM C.69334).

Cardiolucina pisiformis (Thiele, 1930)

Figs 14–15

Phacoides (Parvilucina) pisiformis Thiele, 1930: 592.
Phacoides (Parvilucina) pisiformis Thiele – Ponder, 1978: 439, pl. 2 figs 3 & 9.
Bellucina pisiformis (Thiele) – Slack-Smith, 1990: 135.

Holotype. Museum für Naturkunde, Berlin. Reg. no. 67726. L= 3 mm, H= 2.9 mm (details from Ponder, 1978).

Type locality. 5 km N.W. of Denham, Shark Bay, Western Australia, 3 m.

Shell description. Shell very small, to a maximum height of 4.4 mm, outline circular, H/L mean 0.97; inflated, T/L mean 0.42, tumidity of single valve to 2.0 mm. Inequilateral, slightly extended anteriorly. Shallow posterior sulcus with concentric lamellae. Lunule heart-shaped, slightly excavated, smooth. Anterodorsal area indistinct. Posterodorsal area with concentric lamellae. Exterior sculpture of 13–17 low, flattened, radial ribs with broad interspaces. Ribs broader and more rounded towards anterior of shell. About 20 thin, concentric lamellae project slightly above radial ribs. Sculpture distinctly fenestrate in appearance. Hinge plate strong. Left valve with single posterior lateral, two cardinal teeth, the posterior of these large and robust, the anterior small. Single anterior lateral tooth. Right valve with a single, strong, posterior lateral tooth, two cardinals, the anterior large and the posterior very small and a single anterior lateral. Ligament extends from beak to posterior lateral tooth. Inner margin with about 13 coarse crenulations, which are sometimes bifurcate with occasional small denticles in the interspaces. Small, rounded denticles around anterior and posterior dorsal margins. Anterior adductor muscle scar elongate, slightly buttressed with only the ventral tip detached from the pallial line. Posterior adductor muscle scar rounded. Pallial line continuous. Shell white.

Juvenile shells (Fig.14 e) are more extended both anteriorly and posteriorly, with a prominent convex anterodorsal area.

Comparison with other species. This is a small distinctive species with an exterior ornament similar to *C. eucosmia* and *C. siquijorensis*. It is smaller, more circular in shape and lacks the deeply-excavated lunule of *C. eucosmia*. *C. siquijorensis* has fewer and broader radial ribs, a shallower lunule and a different dentition.

Habitat. Shallow water to 240 m.

Distribution. Western Australia (Fig. 15).

Material examined. **AUSTRALIA**: **Western Australia**, W. of Rottnest Island, 110m (WAM 262–94); Point Peron Peninsula, Shark Bay (WAM 257–94, 258–94, 259–94, 260–94,); Carnarvon (WAM); N. of Homestead Point, Dirk Hartog Island (WAM 250–94); Ningaloo Reef, N.W. Cape (WAM); Mangrove Bay beach, N.W. Cape (WAM); Yardie Creek to Tantibiddi, N.W. Cape (WAM wet material); N.W. of Port Hedland, 112m (AM C.309462); N.W. Shelf, W. of Roebuck Bay, 238m (AM C.309464); Broome (ANSP 233737); **Northern Territory**, N. of Cobourg Peninsula, 55m (AM); 200km N. of Melville Island, 215m (AM).

Cardiolucina quadrata (Prashad, 1932)

Figs 16–17

Dentilucina (Bellucina) hedleyi var. *quadrata* Prashad, 1932: 164, pl. 5 figs 19 & 20.

Type material. Holotype, one individual two valves, L=10.5 mm, H=10.5 mm. Also 4 paratype valves. (ZMA).

Type locality. Siboga Expedition station 212 (5° 54.5'S, 120° 19.2'E), west of Salayar, Sulawesi, Indonesia, 462 m.

Shell description. Shell solid, small, height to 12.9 mm, subcircular, H/L mean 0.97, moderately inflated, mean T/L 0.38, tumidity to a maximum of 5.3 mm on a single valve. Shell inequilateral, extended anteriorly. Shallow posterior sulcus with concentric lamellae; umbones prominent. Lunule extremely small and shallow. Anterodorsal area heart-shaped, slightly convex with fine concentric lamellae. Escutcheon lanceolate, with fine concentric lamellae and a few radial ribs. Exterior sculpture of about 25 fine, closely spaced, radial ribs which are rounded in profile. Radial ribs crossed by 25–30 low, broad, concentric lamellae, the intersection giving a finely beaded appearance. Hinge plate thick. Left valve with an single posterior lateral tooth, two cardinal teeth, the anterior of which is hooked and sits on a rounded buttress, and a single anterior lateral tooth. Right valve with single posterior lateral, two cardinal teeth with the posterior larger and a single anterior lateral tooth. Ligament elongate extending from beak to two thirds of distance to the posterior lateral tooth. Inner margin with about 25 crenulations, some of those to the posterior bifurcating. Shallow sinus on posterior margin. Anterior adductor muscle scar elongate, not buttressed, slightly detached at the ventral tip from the pallial line. Posterior adductor muscle scar ovate. Pallial line continuous. Shell colour white.

Comparison with other species. Although this species name was first introduced by Prashad (1932) as a variety of *Dentilucina (Bellucina) hedleyi* (= *C. civica*) it is clearly distinct. In many characters, such as hinge teeth, it resembles *C. australopilula*, but differs in shape and external sculpture, the latter having a fenestrate ornament compared with the finely beaded sculpture of *C. quadrata*.

Habitat. A deeper water species from muds at 230–1280 metres.

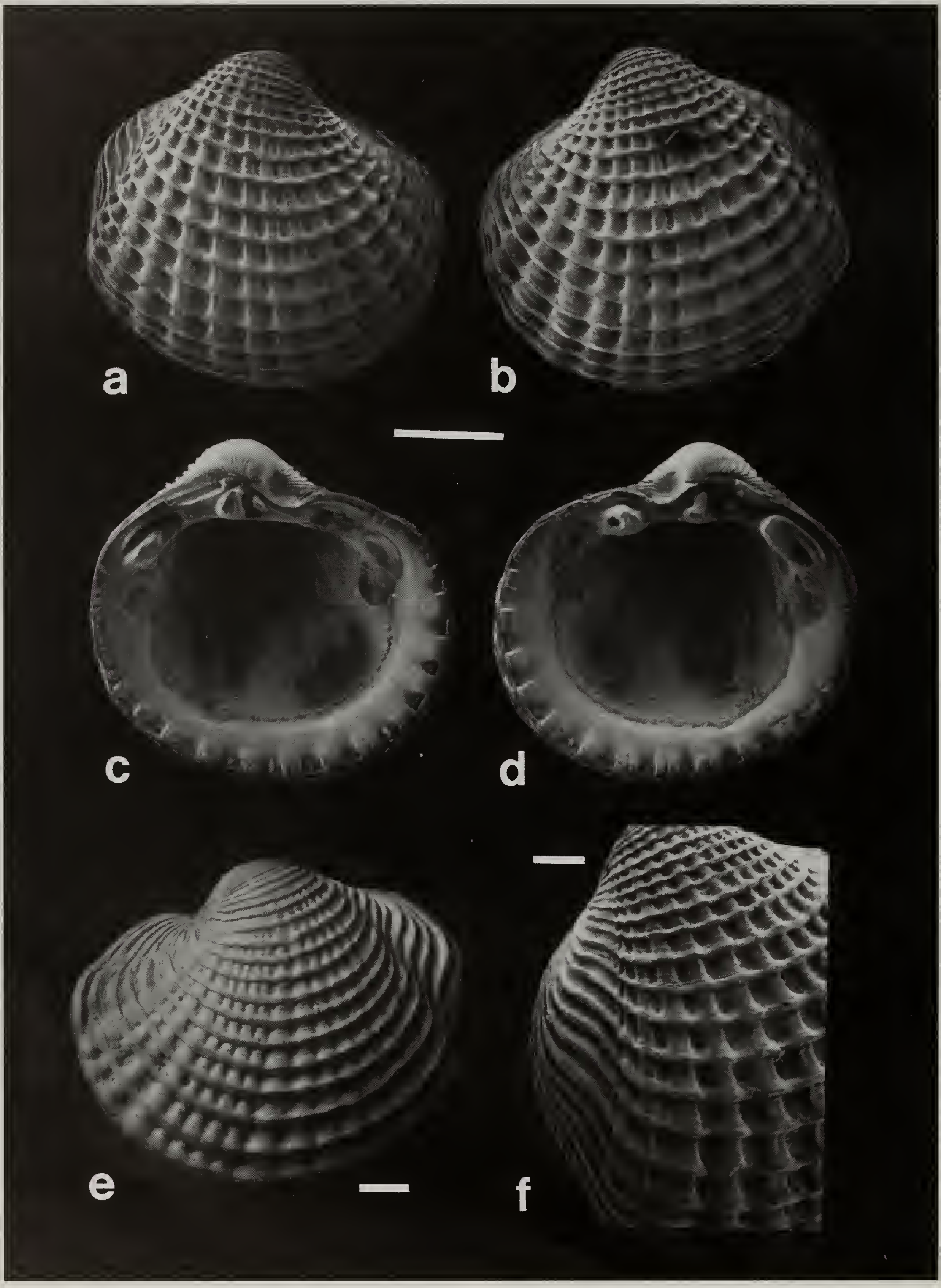

Fig. 14 a–d, f *Cardiolucina pisiformis* (Thiele, 1930) Bandicoot Bay, Barrow Island, Western Australia, WAM 268–94 and Fig. e *C. pisiformis*, Peron Peninsula, Shark Bay, Western Australia WAM 258–94. a, exterior of right valve; b, exterior of left valve; c, interior of left valve; d, interior of right valve; e, juvenile, exterior of shell; f, exterior of shell surface showing posterior sulcus. Scale bars a–d = 1.0mm, e = 500µm, f = 300µm.

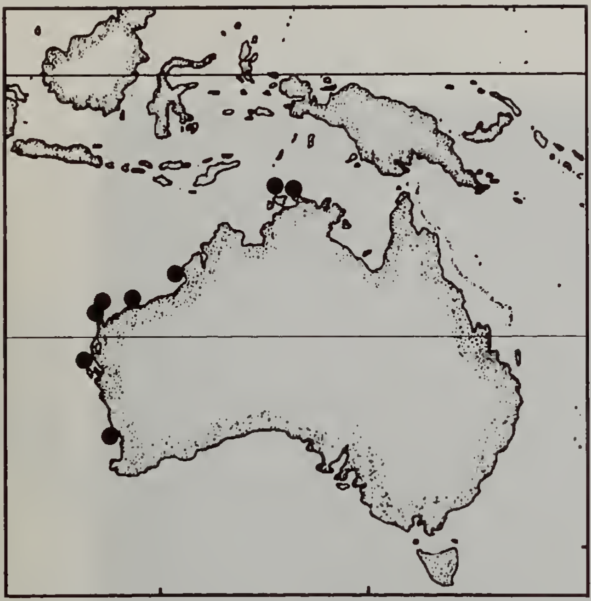

Fig. 15 Geographical distribution of *Cardiolucina pisiformis* (Thiele).

DISTRIBUTION. Indonesia and Philippines (Fig. 17).

MATERIAL EXAMINED. **INDONESIA**: Kai Islands, 05°23'S 132°37'E, 436–413m & other stations in same area between 250–450m (MNHN, Bouchet and von Cosel manuscript). **KALIMANTAN**: Sibuko Bay, 762 & 589m (USMN 302240). **PHILIPPINES**: 11°58'N 122°02'E, 486–551 m (MNHN) (see Cosel & Bouchet, ms.); off Baliscasag I., S. Bohol, 812m (USNM 298742); Iligan Bay, N. Mindanao, 500m (USNM 298616) & 505m (USNM 298660); off Claveria, Burias, 390m (USNM 2800546); off N. Ticao I.,420m (USNM 298025); off Ponson I., Camotes Islands, 650m (USNM 298468); off Apo I., S. Negros, 460m (USNM 298759); Sogod Bay, Leyte, 1280m (USNM 298560).

Cardiolucina rugosa (Hedley, 1909)

Figs 18–19

Lucina (Myrtea) seminula Gould, 1862: 174 (non *Lucina seminulum* Deshayes, 1858: 673).
Lucina (Codakia) seminula (Gould) – Smith, 1885: 180–181, pl. 13, figs 5 & 5a.
Phacoides rugosus Hedley, 1909: 427.
Lucina seminula Gould – Johnson, 1964: 148, pl. 28 fig. 3.

TYPE MATERIAL. Lectotype selected by Johnson (1964, pl 28 fig. 3) (USNM 553). Hedley (1909) introduced the replacement name *P. rugosus* because *L. seminula* is preoccupied. The specimen from the type locality illustrated in Fig. 18 was given by Gould to Cuming.

TYPE LOCALITY. Hong Kong Harbour, 9–18 m.

SHELL DESCRIPTION. Shell solid, small, height to a maximum of 3.1mm, subcircular in outline, H/L mean 0.92; moderately inflated, T/L mean 0.38, tumidity to a maximum of 1.2 mm on a single valve. Shell inequilateral and extended towards anterior. Pronounced posterior sulcus with concentric lamellae. Anteriorly, there is a narrow sulcus. Lunule small, heart-shaped. Anterodorsal area shallowly concave with fine concentric lamellae. Escutcheon lanceolate and slightly convex. Exterior sculpture of about 20 thick, slightly recurved, concentric lamellae. Interspaces between concentric lamellae are variable in width. Concentric lamellae often extended into short flanges at margin of posterior sulcus. Radial ribs indistinct, flattened and closely spaced. Hinge plate thick. Left valve with single posterior lateral, two cardinal teeth, the anterior of which is thicker and triangular and a single anterior lateral. Right valve with a single posterior lateral tooth, two cardinal teeth, the posterior large and the anterior a thin plate, with a single anterior lateral tooth. Ligament very short, extending from beak to less than half way to posterior lateral tooth. Inner margin with 20–21 sharp crenulations. Small denticles on posterior and anterior dorsal margin. Shallow sinus on posterior margin corresponding to the position of the posterior sulcus. Anterior adductor muscle scar elongate, not buttressed, detached from the pallial line only at the ventral tip. Posterior adductor muscle scar ovate. Pallial line continuous. Shell colour creamy white.

COMPARISON WITH OTHER SPECIES. *Cardiolucina rugosa* is closely similar to *C. semperiana*, but it is smaller, less tumid with more prominent, recurved concentric lamellae and greater anterior extension.

HABITAT. 10–250 m with a few dead shells from 540 m, sublittoral silts and muds.

DISTRIBUTION. Queensland, Australia to Hong Kong (Fig. 19).

MATERIAL EXAMINED. **HONG KONG**: North Lantau (BMNH; BMNH 1963233; NMW acc. 55.158; AM C.33806; 9–18m (USNM 611842, 2 paratypes); (USNM 24252); (USNM 714821). **CHINA**: off Pratas Islands, 268m (USNM 296955). **KALIMANTAN**: off Silungan I., 539m (USNM 291027). **PHILIPPINES**: (USNM 21109); Pescador I. Tanon Straits, 412m (USNM 293876); Bohol (BMNH); off Sombrero I., Balayan, 216m (USNM 312342); S.E. of Bantayan I., 60m (USNM 293115); Destacado I., 218m (USNM 298090); off N. Cebu, 125m(USNM 293266); Pujada R., E. Mindanao, 253m (USNM 294765); off Tochanhi Pt, Tawi Tawi Islands, 90m (USNM 292997) & 35m (USNM 283372); 11°43'N, 122°34'E, 93–99m (MNHN). **AUSTRALIA**: **Queensland**, Cape York (BMNH 1887.2.9.2772–5); Hope Islands, 10–18m (BMNH 1910.9.28.68–71 and BMNH 1963259); Palm Island (NMW acc. 55.158); Gulf of Carpentaria 16°58'S 140°53'E, 9m (AM C.015275); Albany Passage, Torres Strait, 9–30m (AM C.36171); Palm Island (AM C.1049); Low Isles, 27m (AM); Cape Sidmouth (AM C. 2594); Endeavour Reef, 40m (AM C.44668); Hervey Bay (AM); Barney Point, Port Curtis (AM C.21805); Facing Island (AM C.4428); Quoin Island, Port Curtis (AM); **Northern Territory**, Darwin (AM). **PAPUA NEW GUINEA**: 0.5 mile off Fairfax Harbour, Port Moresby, 15–18m (AM C.309466).

Cardiolucina semperiana (Issel, 1869)

Figs 21–24

Lucina pisum Reeve 1850 (part), pl. 11, fig. 66b (non *L. pisum* Sowerby 1836).
Lucina semperiana Issel, 1869: 82–83.
Phacoides (Bellucina) semperiana (Issel) – Lamy 1920: 211–213.
Dentilucina (Bellucina) macassari Prashad 1932: 163 pl. 5 figs 13–16.
Lucina semperiana (Issel) – Bouchet & Danrigal 1982: 16, fig. 19.
Bellucina semperiana (Issel) – Oliver 1992: 99, pl. 19 fig. 7.

TYPE MATERIAL. The species concept of *C. semperiana* was based on the figure in Savigny (1817, pl. 8, fig 12) and one specimen from Suez in the Issel Collection (now lost); the single shell of this species in the Savigny collection (MNHN) illustrated by Bouchet & Danrigal

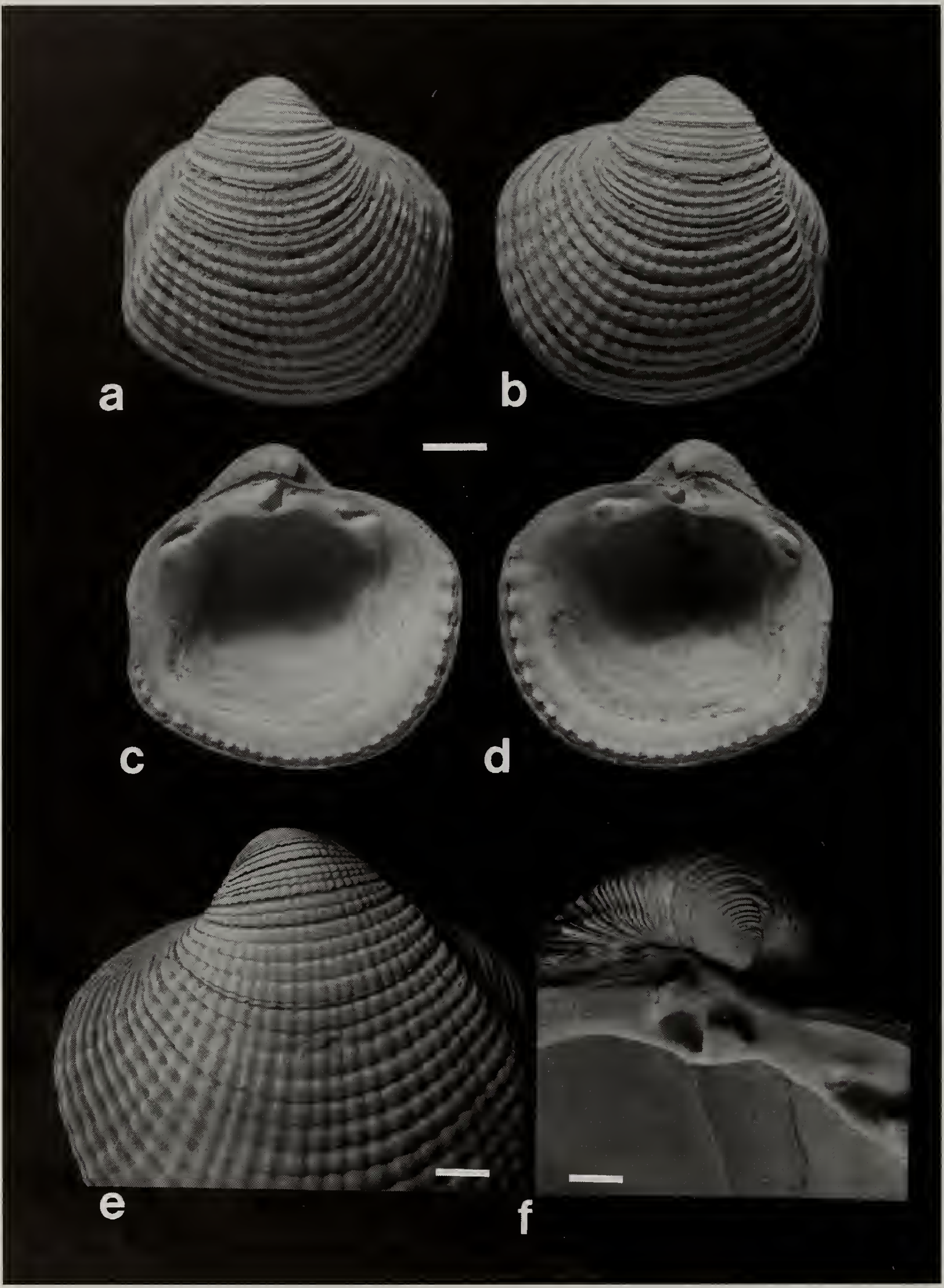

Fig. 16 *Cardiolucina quadrata* (Prashad, 1932). a–d, holotype of *Dentilucina (Bellucina)* var. *quadrata* Prashad, 1932, Salayar, Sulawesi, Indonesia and e–f, *C. quadrata*, Kai Islands, Indonesia, BMNH. a, exterior of right valve; b, exterior of left valve; c, interior of left valve; d, interior of right valve; e, exterior shell surface; f, hinge showing hooked anterior cardinal tooth in the left valve. Scale bars a–e = 2.0mm, f = 1.0mm.

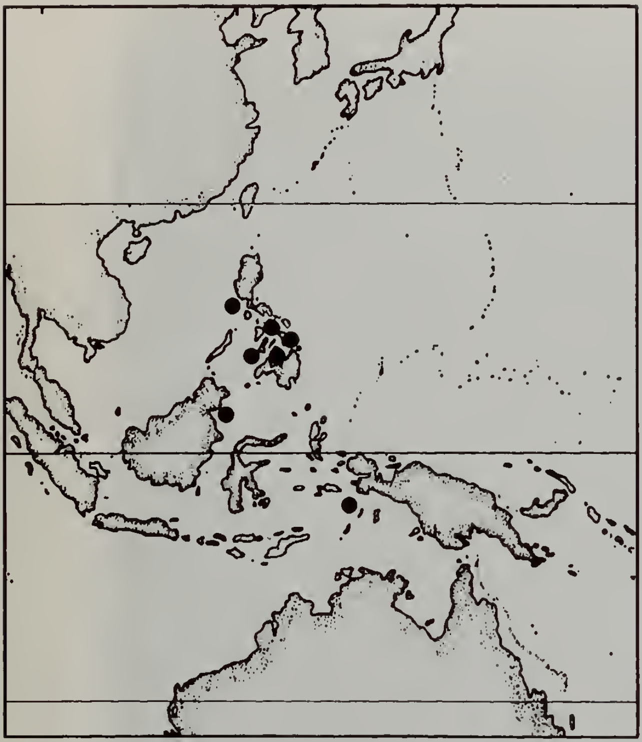

Fig. 17 Geographical distribution of *Cardiolucina quadrata* (Prashad).

(1982, fig. 19) is here designated as lectotype. The holotype of *Dentilucina (Bellucina) macassari* Prashad is located at ZMA, reg. number 3.32.090 (Fig. 21 c & d).

TYPE LOCALITY. *C. semperiana* from Suez, Red Sea. *C. macassari* from Makassar, South Sulawesi, Indonesia (Siboga Expediton station 71).

SHELL DESCRIPTION. Shell solid, small, height to a maximum of 7.7 mm, sub-circular in outline H/L mean 0.98; inflated, T/L mean 0.46, tumidity of single valve to 4.6 mm. Inequilateral, extended anteriorly. Deep sulcus posteriorly with prominent concentric lamellae. Posterodorsal margin of the sulcus marked by a ridge with prominent short lamellae. Lunule heart-shaped, shallow. Anteriorly, there is a narrow sulcus. Escutcheon lanceolate with fine concentric sculpture. Exterior sculpture of 20–30 low, rounded radial ribs with narrow interspaces. These are crossed by 15–24 projecting, concentric lamellae which are often irregularly spaced. In some specimens, concentric lamellae are thickened with steep, ventral edges, giving a stepped appearance to the shell. Hinge plate thick. Left valve with single posterior and anterior lateral teeth and two cardinal teeth, of

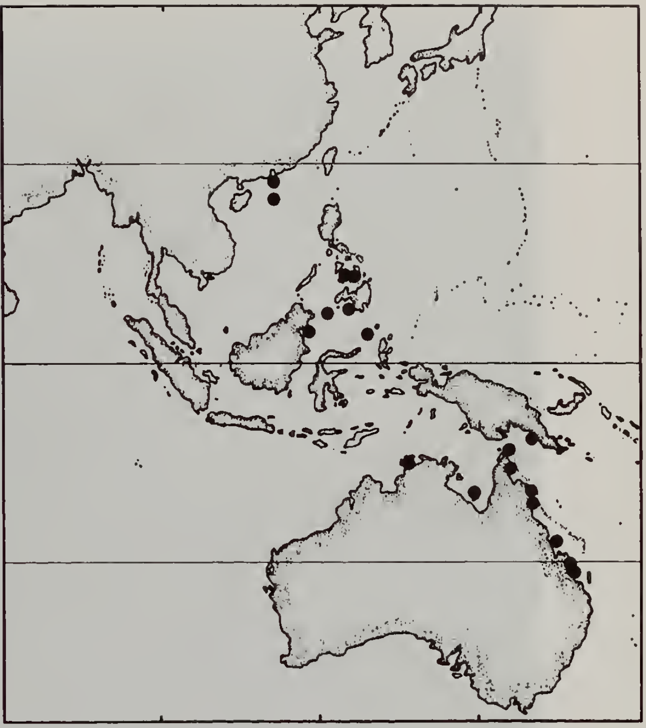

Fig. 19 Geographical distribution of *Cardiolucina rugosa* (Hedley).

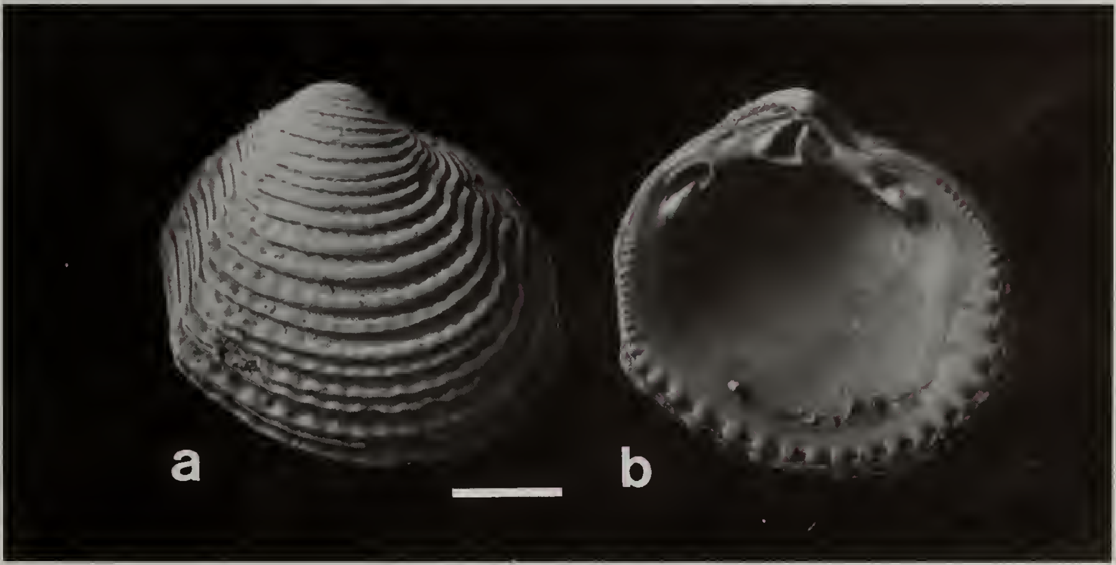

Fig. 18 *Cardiolucina rugosa* (Hedley, 1909), Hong Kong Harbour, BMNH 1963233. Specimen of *Lucina seminula* Gould 1862 from type locality, given by Gould to Cuming. a, exterior of left valve; b, interior of right valve. Scale bar a–b = 1.0mm.

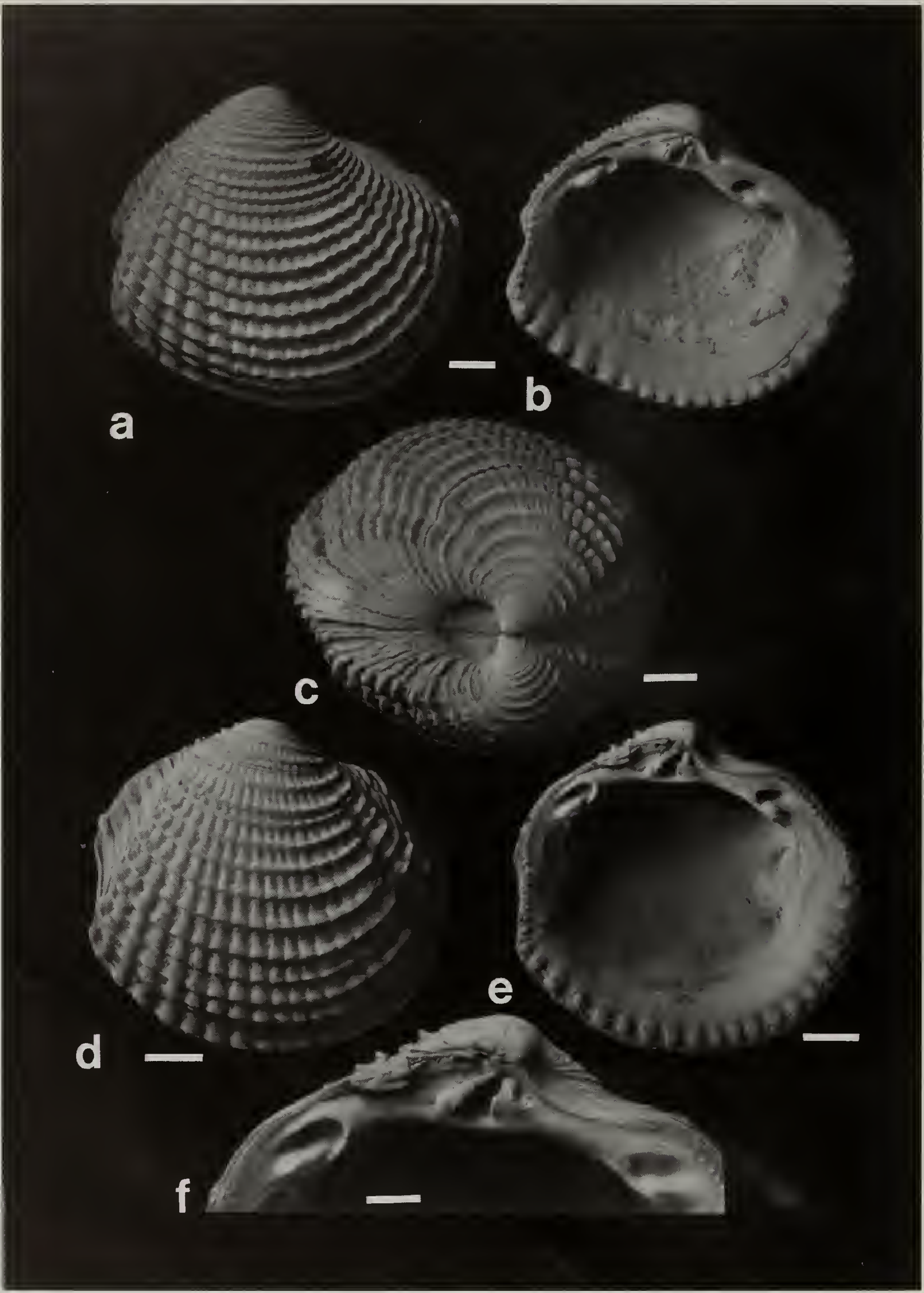

Fig. 20 a–b *Cardiolucina semperiana* (Issel, 1869), Gulf of Suez, Red Sea BMNH 1870.1.19.4, c–f *C. semperiana,* Tuléar, Madagascar, BMNH. a, exterior of right valve; b, interior of left valve; c, dorsal view articulated shell; d, exterior of right valve; e, interior of left valve; f, hinge showing details of the dentition with denticulate posterior cardinal tooth. Scale bars a–b = 1.0mm, c = 750μm, d–e = 1.0mm, f = 500μm.

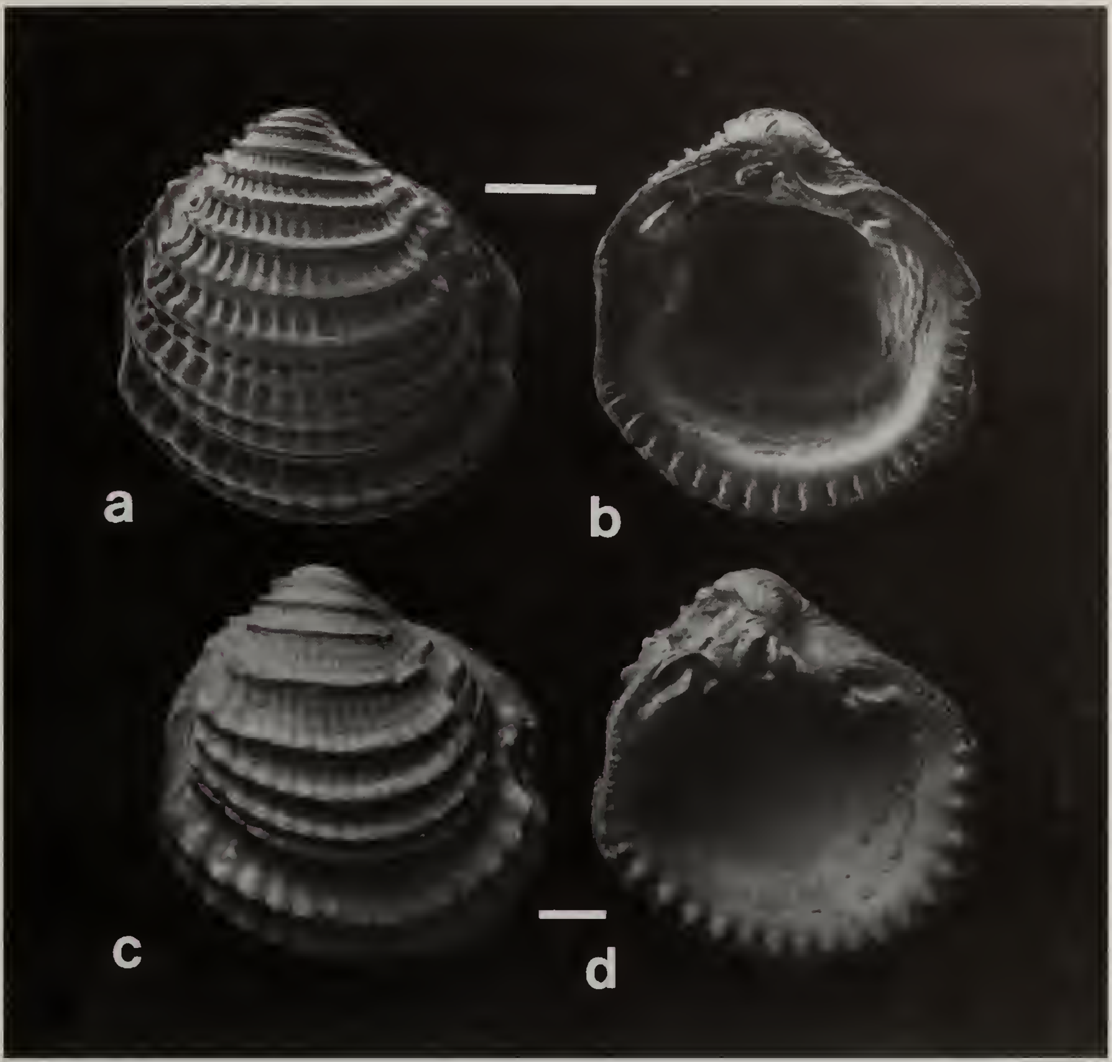

Fig. 21 *Cardiolucina semperiana* (Issel, 1869). Figure a–b Paralectotype of *Lucina pisum* Reeve, 1850 BMNH 1963552, Singapore and c–d Holotype of *Dentilucina (Bellucina) macassari* Prashad, 1932, Makassar, Indonesia, ZMA. a, exterior of right valve; b, interior of left valve; c, exterior of right valve; d, interior of left valve with attempted drill hole on the posterior part of the umbo. Scale bars a–d = 1.0mm.

which the anterior is the smaller. Right valve with single posterior and anterior laterals and two cardinals, the posterior being the larger. Cardinal teeth have small denticles. Ligament extends two thirds of the distance from the beak to the posterior lateral tooth. Inner margin with 20–21 crenulations and there are also small, rounded denticles along anterodorsal and posterodorsal margins. Both anterior and posterior shell margins have shallow sinuses corresponding to the sulcii. Anterior adductor muscle scar elongate, buttressed in the more tumid specimens, detached from the pallial line only at the ventral tip. Small pedal retractor muscle scar at dorsal tip of anterior adductor scar. Posterior adductor muscle scar ovate. Pallial line continuous. Shell creamy white.

ANATOMY. (Fig. 22) Posterior inhalant aperture absent, exhalant aperture a small inverted tube. Ctenidia large and thick, inner demibranchs only, with a thin, shallow, ventral food groove. Gill filaments long and broad, with large central space crossed by transverse muscle strands (Fig. 22 c). Bacteriocyte zone packed with ovoid bacteria about 2.0–2.5 µm in length (Fig. 22 d). Labial palps consist of small papilla at edge of lips. Foot cylindrical, vermiform, with a much-corrugated outer surface, a pointed tip and a small rounded heel to the posterior. Ctenidia attached to posterior mantle by a thin muscular sheet (Fig. 22 f). Body wall with a large irregular visceral pouch in the antero-ventral position.

GEOGRAPHICAL VARIATION. This species is extremely variable both within populations and across its range from the northern end of the Red Sea to the Philippines. In Southeast Asia *semperiana* are generally smaller, but relatively more tumid, as shown in Fig. 23, which plots ratio of length over tumidity against mean height of specimens from Red Sea, Madagascar, India, South East Asia. The holotype of *macassari* is the most tumid of all the specimens measured, but is probably an abnormal individual which has survived attempted drilling at the posterior dorsal margin. *C. semperiana* from Southeast Asia also tend to have fewer, but heavier, concentric lamellae (Figs. 21).

HABITAT. Live material collected from shallow water (up to 50 m), a few dead shells from up to 350 m, mud and sand.

COMPARISON WITH OTHER SPECIES. *C. semperiana* is similar to *C. rugosa* but is larger, more tumid and has more prominent radial ribs.

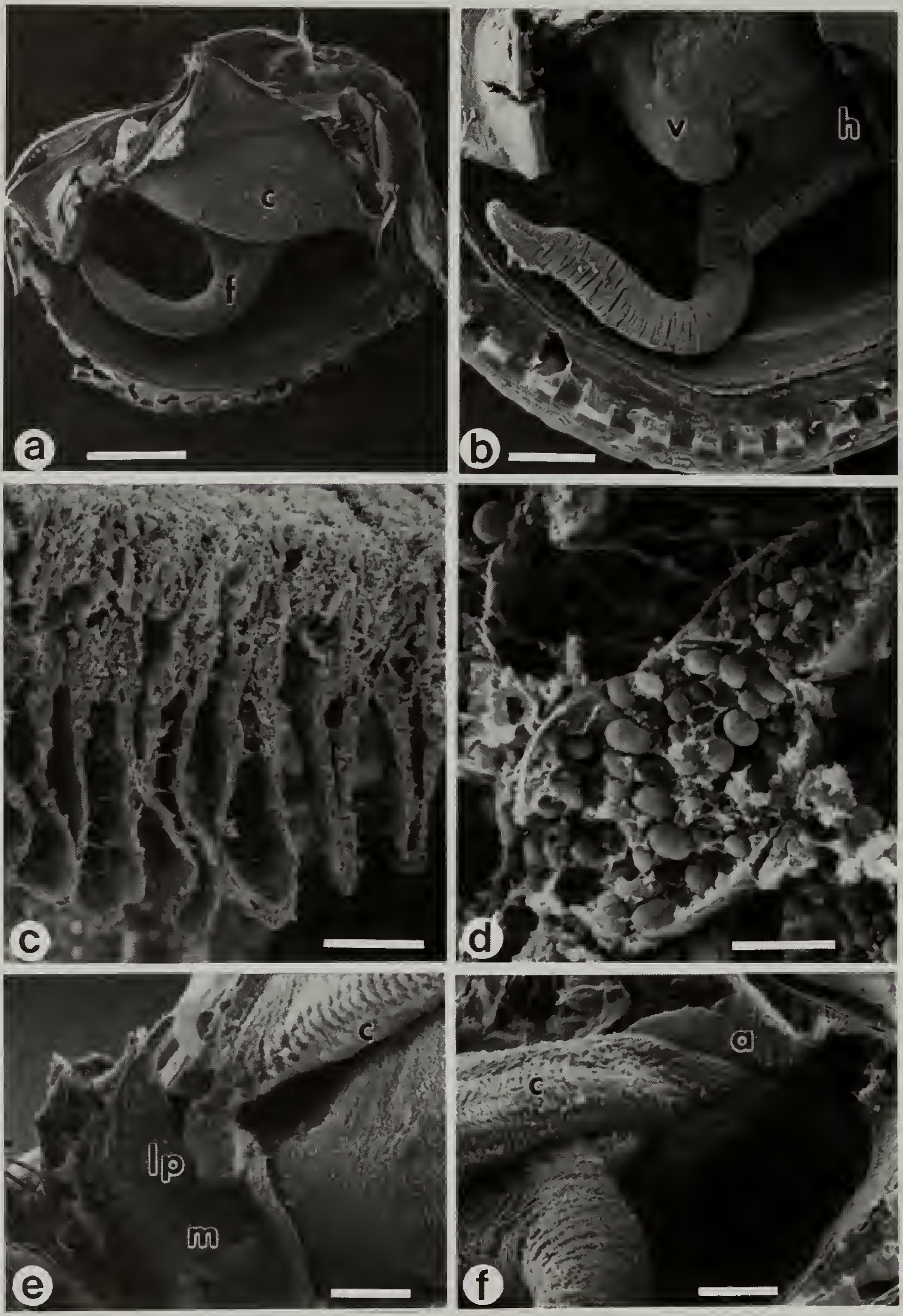

Fig. 22 *Cardiolucina semperiana* (Issel, 1869), Sinai Coast, Gulf of Suez, Egypt. NMW 1982.068. a, interior of right valve showing thick inner demibranch of the ctenidium and cylindrical, vermiform foot; b, right valve showing pronounced visceral pouch and the foot with strongly corrugated surface and small, rounded heel; c, section showing broad gill filaments and transverse muscle strands crossing the spaces within the filaments. d, bacteriocyte zone with ovoid bacteria; e, labial palps (lp) and mouth (m); f, ctenidia attached to the posterior mantle by a thin muscular sheet. Abbreviations: c=ctenidium, f=foot, v=visceral pouch, h=heel, lp=labial palps, m=mantle, a=attachment of ctenidium to mantle. Scale bars a = 1.0mm, b = 500µm, c = 40µm, d = 5µm, e = 150µm, f = 250µm.

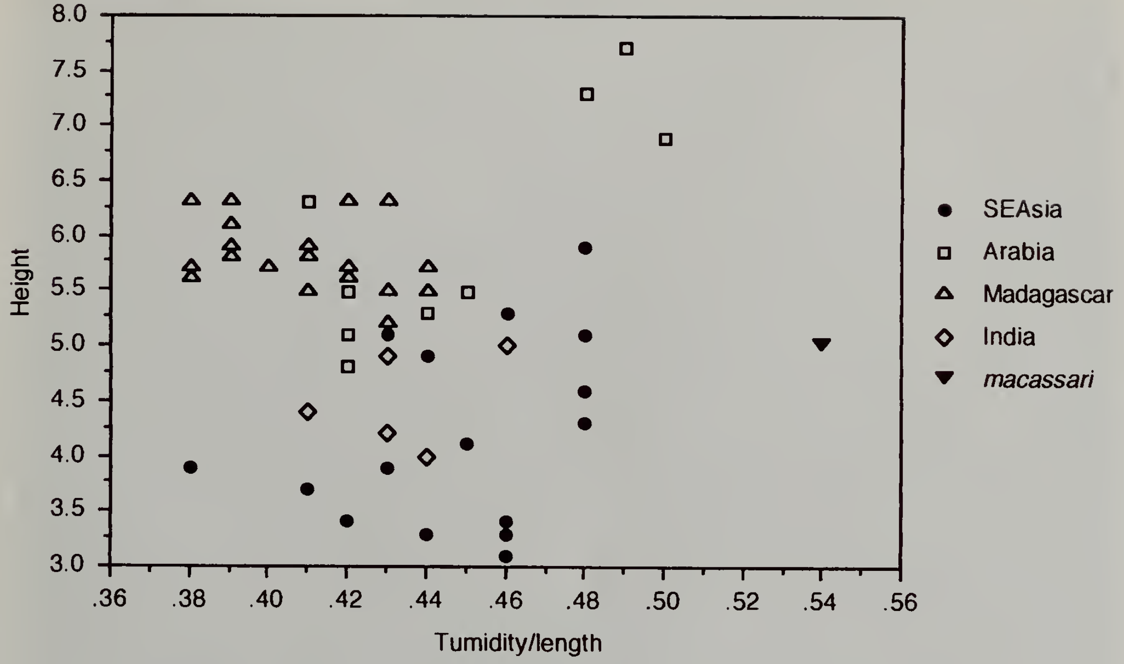

Fig. 23 Geographical shape variation of *Cardiolucina semperiana*. The specimen of *C. macassari* is the holotype.

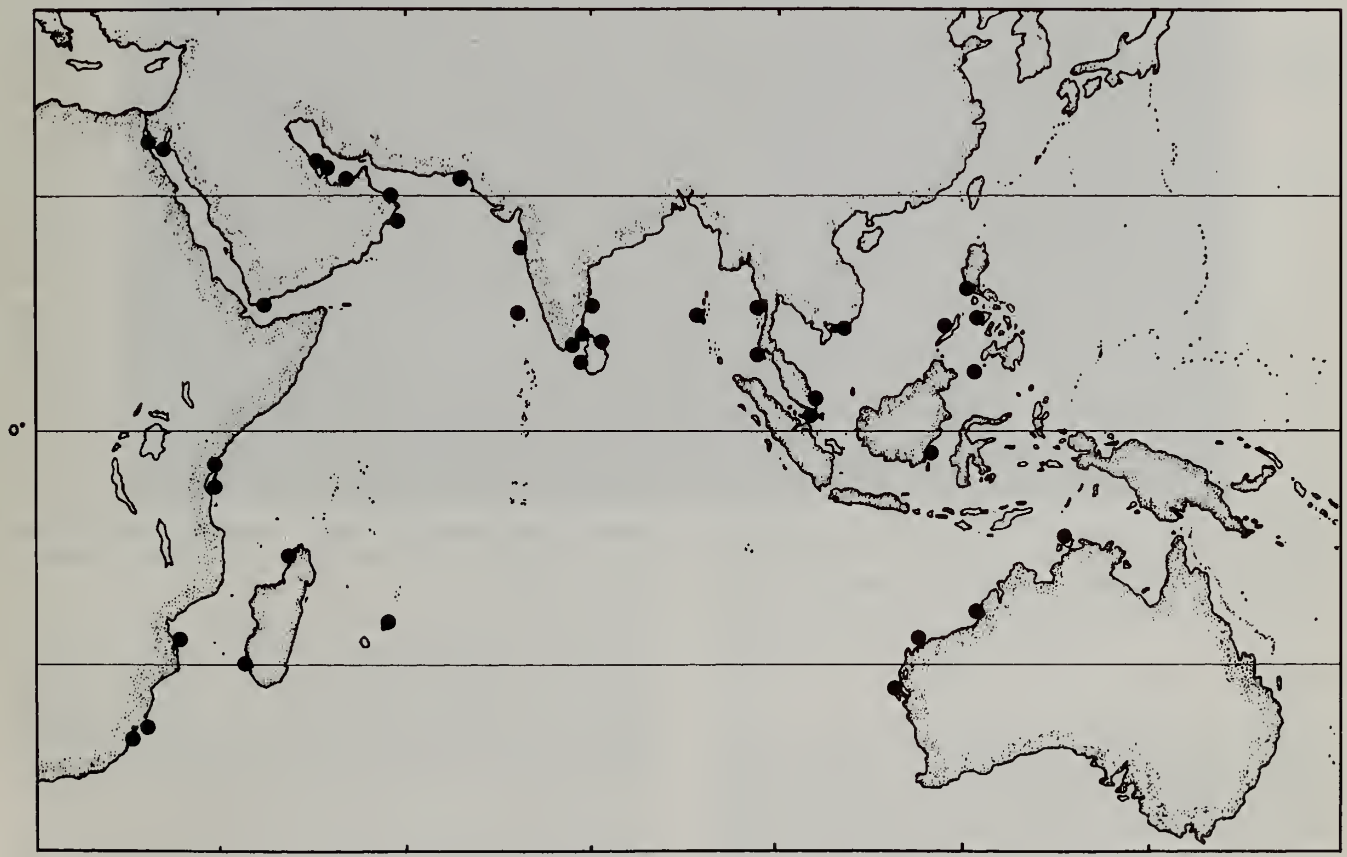

Fig. 24 Geographical distribution of *Cardiolucina semperiana* (Issel).

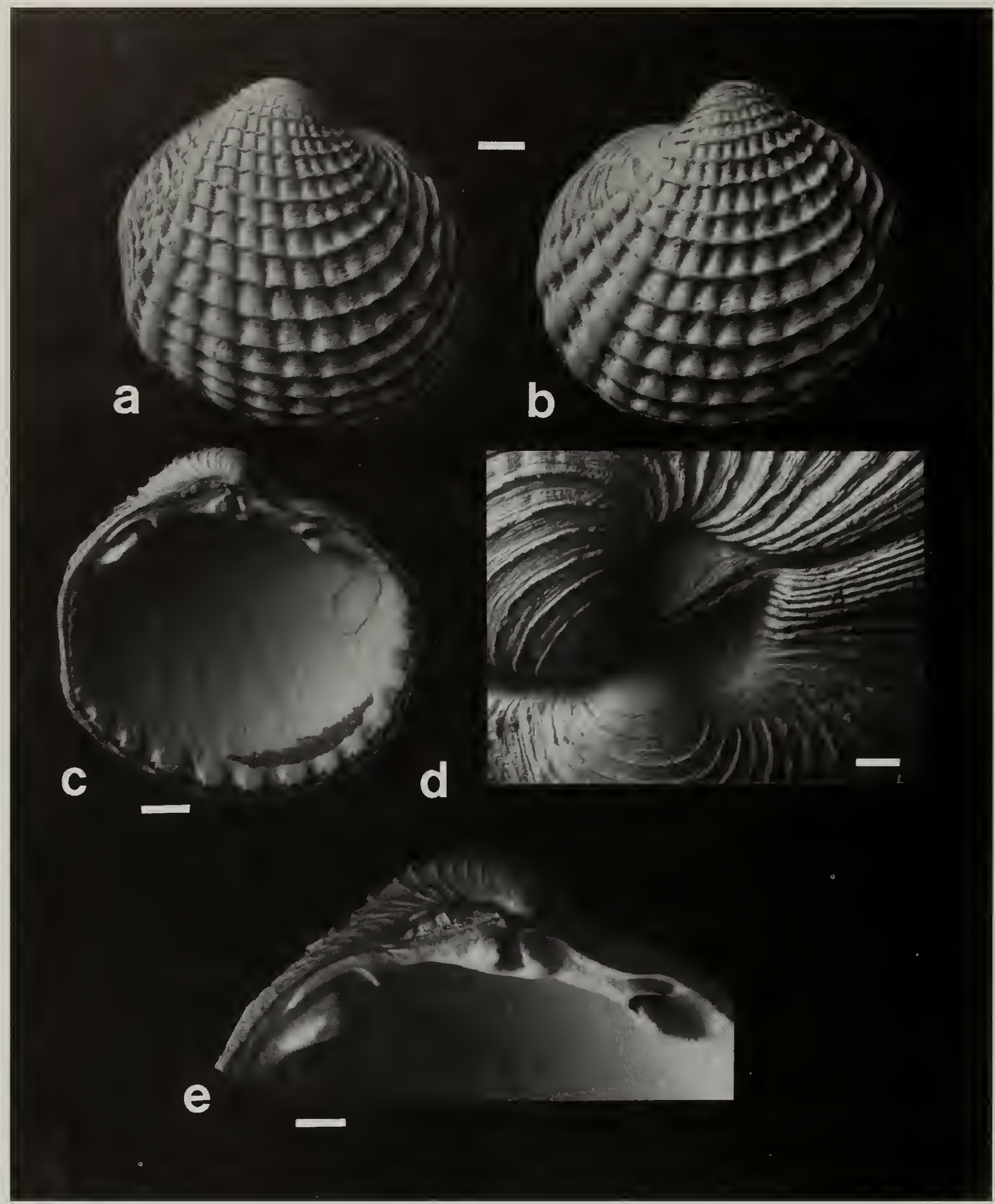

Fig. 25 *Cardiolucina siquijorensis* Taylor and Glover new species, Siquijor, Philippines. a, Paratype (USNM 812176), exterior of right valve; b, Holotype (USNM 812176), exterior of left valve; c, Paratype, interior of left valve; d, Holotype, detail of lunule; e, Paratype, hinge of left valve showing posterior lateral tooth with pronounced rim on the socket. Scale bars a–c = 500µm, d = 150µm, e = 250µm.

DISTRIBUTION. Northern Red Sea, southern Africa to Philippines (Fig. 24).

MATERIAL EXAMINED. **EGYPT**: Gulf of Suez (BMNH 1870.1.19.4); Suez (BMNH 1963492); Nuweiba, Sinai (AM 1954). **YEMEN**: Aden (BMNH 1902.12.30.754–6 & 1963235); Aden (AM C.33727); (USNM 608854). **OMAN**: Qurm, Muscat (NMW Z.1993.061.0434); Masirah (NMW Z.1993.061.0427 & 0433). **ARABIAN GULF**: (USNM 636963); Bahrain (NMW 1993.061.043); Linyah (NMW acc. 55.158); Qatar (BMNH acc. 2258); Abu Dhabi (BMNH). **ZANZIBAR**: Nyange I., 20m (ANSP 251213); 1.5 miles S.W. of Ras Shangani, 18–20m (ANSP 213493); 1 mile N. Bawi I., 22m (ANSP 250912). **KENYA**: Mombasa (BMNH acc. 2223), (NMW 1955.158). **TANZANIA**: Msimbasi Bay, Dar es Salaam 5m (AMC.309448).**MOZAMBIQUE**: Bazaruto I., 8–10 m (NM K5317 & G4458). **SOUTH AFRICA**: Durban Bay, (NM E834 & A2357); Shelly Beach, Izotsha, Natal (NM9898). **MADAGASCAR**: N.W. Madagascar, 30m (AM C.70660); Tuléar (MNHN); 40 miles W.S.W. Tuléar, 33m (USNM 761189); Nossi Bé (USNM 633927); Nossi Bé, shallow water to 35m, (ANSP 261127, 259587, 259028, 260541, 261338, 259901, 261873). **MAURITIUS**: 1.5 m N.W. Black River, 15m (ANSP 273431). **PAKISTAN**: Karachi (BMNH acc. 1831). **INDIA**: 80 miles S.W. Bombay 17° 54'N 72 °27'E, (USNM 716676); Madras (BMNH 1953.1.30.190–4); Madras (BMNH 89.2.17.23–6); Tondi, Madras (NMW acc 55.158); Manapad (BMNH 1953.1.30.26); Mandapam, Gulf of Mannar, 3m (ANSP 302433); Tuticorin (BMNH 1953.1.30.188–89); S. of Krusadai I., Gulf of Mannar, 18m (ANSP 301196); Andaman Islands (AM C.040397, C.040597); Andaman Islands (NMW 55.158). **SRI LANKA**: Colombo (AM); Trincomallee, 29m (AM); E., S., and N. coasts (AM C.309467); BMNH 1963491; Palk Strait, 22m (AM); 9°34.5'N 80°39'E (AM C.309461); northern tip of Eluvativu I., (ANSP 211085). **BURMA**: 57 miles N.W. Tavoy I., Anadamans Sea, 39m (ANSP 293254). **THAILAND**: Koh Kahdat(AM C.031287); Phuket (USNM 661156); south end Lighthouse I., Phuket, 5m (ANSP 286500); 25 miles N.N.W. Phuket, 42m (ANSP 291734). **MALAYSIA**: Mersing Island, E. Malaya, 3.5m (AM). **SINGAPORE**: BMNH acc. 2172; Singapore (AM C.3437); NMW acc 55.158. **INDONESIA**: Kalimantan (AM C.309470). **PHILIPPINES**: Corregidor, Bay of Manila, intertidal (BMNH; Manila Bay, 18m (ANSP 281443); Manila Bay, 18m (ANSP 328655); off Antonia I., E. Panay, 40m (USNM 293697); N. of Marinduque, 353m (USNM 295197); Lataau I., 33m (USNM 236058); Malampaya Sound, Palawan, 25–35m (USNM 297395); off Tinkata I., Tawi Tawi Islands, 30m (USNM 257677); **VIETNAM**: VungTau, Chilins (ANSP 330797). **AUSTRALIA**: **Western Australia**, Shark Bay (AM C.69245); Carnarvon, 7.6m (AM); Carnarvon (AM C.69270); 210 miles N. of Broome, 230m (AM); 110 miles N. of Melville Island, Arafura Sea (AM); 72 miles N.W. of Dampier Island, 110m (AM 2405).

Cardiolucina siquijorensis Taylor and Glover, new species

Fig. 25

TYPE MATERIAL. Holotype, articulated specimen (Fig. 25 b) USNM 812176. H= 3.4 mm, L=3.5 mm. Paratypes, USNM 812177, 812169.

TYPE LOCALITY. Siquijor, Solong-on, Siquijor I., Visayan Islands, Philippines (09° 13'10"N 123° 27'30"E) depth 2–3 m.

SHELL DESCRIPTION. Shell very small, to a maximum height of 3.5 mm, outline circular H/L 0. 97, inflated, T/L 0.39, tumidity of single valve to 1.3 mm. Shallow posterior sulcus with concentric lamellae. Anterior sulcus absent. Lunule shallow, heart-shaped. Anterodorsal area indistinct, posterodorsal area with concentric lamellae. Exterior sculpture, fenestrate, of 11–12 broad, straight-sided, radial ribs. Interspaces wide, but narrower than the ribs. Ribs are slightly broader towards the anterior. About 14–16 thin, concentric lamellae, project slightly above radial ribs. Hinge plate robust. Left valve with single posterior lateral tooth, the dorsal edge of the socket extended into a sharp rim (Fig. 22 e); two cardinal teeth, triangular in shape and more or less equisized; single anterior lateral tooth. Right valve with single anterior lateral tooth, a single central cardinal tooth and a robust posterior lateral tooth. Ligament extends from beak to the dorsal end of the posterior lateral tooth (Fig. 22 e). Inner margin with 12 coarse crenulations, and fine beading extending to the hinge margins. Anterior adductor muscle scar elongate, not buttressed, with only ventral tip detached from pallial line. Posterior adductor muscle scar rounded. Pallial line continuous. Shell creamy white.

COMPARISON WITH OTHER SPECIES. This species is similar in size and ornament to *C. pisiformis* but is distinguished by fewer and broader radial ribs, the shallower lunule, the two equal-sized cardinal teeth in the left valve and the single cardinal in the right valve.

HABITAT AND DISTRIBUTION. As for type locality.

MATERIAL EXAMINED. **PHILIPPINES**: Siquijor I., collected with type material (USNM 812177, 812176, 812169).

Cardiolucina sp.

Fig. 26

In addition to the species described, we have four lots from the Philippines consisting of rather badly preserved, disarticulated shells and two rather better preserved juvenile shells. These are distinct in a number of shell characters from the other *Cardiolucina* species. Because the adult specimens are badly preserved and because juveniles often differ considerably from adults, we are reluctant to describe a new species based on this material.

The adult shells have maximum height of 10.8mm, with tumidity of a single valve to 2.7mm and H/L 0.98, T/L 0.5. The posterior sulcus is broad and shallow, the anterior sulcus absent. About 17–18 prominently scalloped, concentric lamellae, with more than 20 fine, rounded, radial ribs, which do not cross the concentric lamellae. The interspaces between the ribs are narrow, but relatively deep and the intersection of the concentric and radial ornament produces a deeply-pitted appearance. The lunule is heart shaped and relatively deep. In the left valve, there is a single posterior lateral, two triangular cardinal teeth, and a single posterior lateral. The inner margin of the shell has about 25 crenulations.

This species is similar to *C. semperiana* but can be distinguished by the lack of the anterior sulcus, the shallower posterior sulcus, the pitted appearance of the shell surface and the more rounded anterodorsal area.

MATERIAL EXAMINED. **PHILIPPINES**: off Sibugay I., E. of Masbate, 198 m (USNM 292666); Daram Channnel, W. Samar, 48 m (USNM 292830); off Matocot Point, W. Luzon, 400 m (USNM 295706); off Corregidor Light, 73 m (USNM 294200).

ATLANTIC OCEAN SPECIES

Cardiolucina lamothei (Dautzenberg, 1913)

Figs 27 a & b, 28

Lucina lamothei Dautzenberg, 1913: 100–101, pl. 3 figs 50–54.
Phacoides (Parvilucina) congoensis Thiele & Jaeckel, 1931: 220–221, pl. 4 fig. 91.
Phacoides (Bellucina) lamothei (Dautzenberg) – Lamy 1920 : 215.

TYPE MATERIAL. Figured specimens of *L. lamothei* – two syntypes from Tamara, Archipel de Los, Guinée, marked TYPE in Dautzenberg's handwriting (MNHN). Numerous other specimens from localities mentioned by Dautzenberg (1913) are housed in the Royal Belgian Institute of Natural Sciences (IRSNB inventory I.G. 10591). Our figured specimen is from a sample sent by Dautzenberg to Tomlin (NMW 1955.158).

TYPE LOCALITY. West Africa, Tamara, Archipel de Los, Guinée.

SHELL DESCRIPTION. Shell solid, very small, height to maximum of 4.0 mm. Subquadrate, inequilateral, slightly extended anteriorly. Not inflated. Anterior sulcus shallow leading to marginal sinus. Umbones are conspicuous, prosogyrate. Lunule very small, underneath beaks. Anterodorsal area indistinct and slightly convex. Escutcheon with concentric lamellae. Exterior sculpture of 15–18 prominent, narrow concentric lamellae, which are slightly reflexed. About 40 fine, radial ribs in the interspaces between concentric

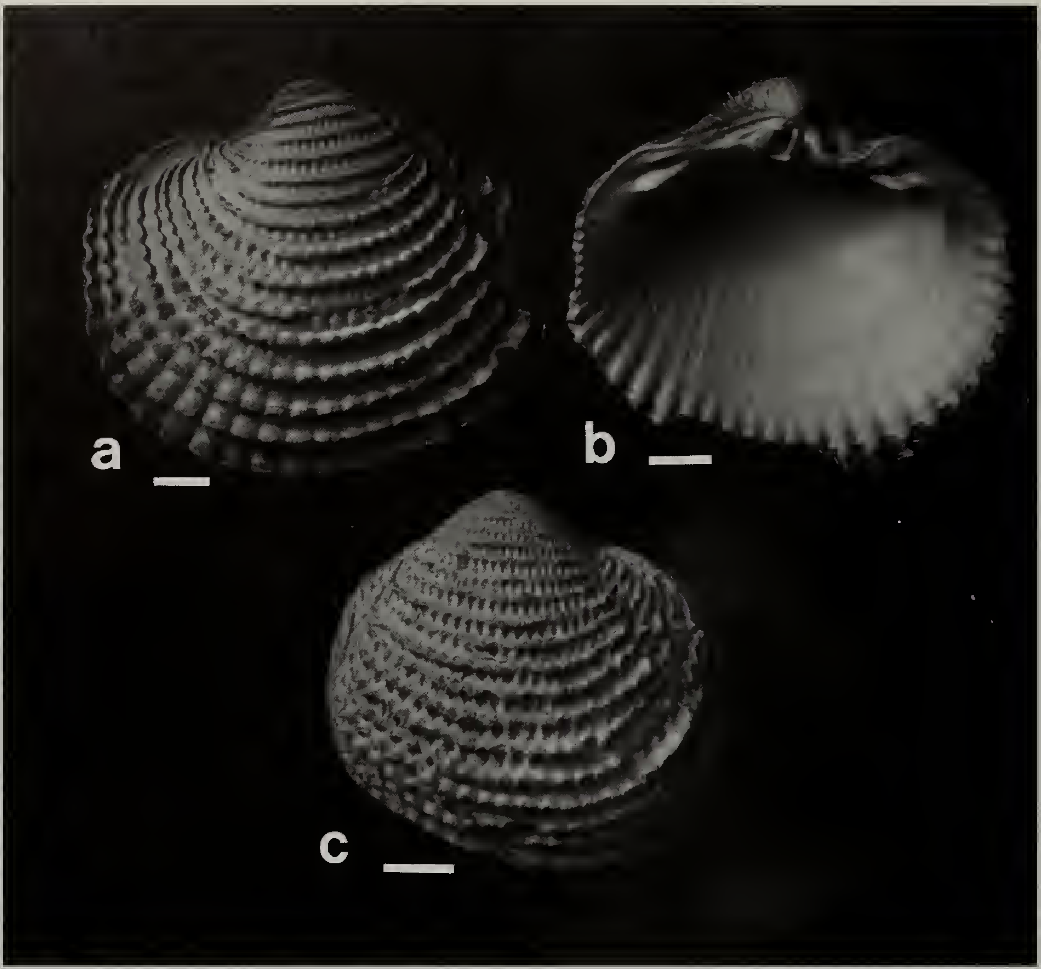

Fig. 26 a–b, *Cardiolucina* sp. Corregidor, Philippines (USNM 294200); c, *Cardiolucina* sp Sibugay Island, Masbate, Philippines (USNM 29266). Scale bars a = 400μm, b = 500μm, c=1mm.

lamellae. Hinge plate thick. Left valve with single, hooked anterior lateral tooth, two cardinals and single posterior lateral tooth. Right valve with similar. Indentations on both anterior and posterior margins which correspond to the position of sulci. Inner margin with about 40 crenulations. Anterior adductor muscle scar elongate, not buttressed. Pallial line attached to lower third of anterior adductor muscle scar. Posterior adductor scar reniform in outline. Pallial line continuous. Shell colour grey-white.

Comparison with other species. This species is similar to *C. rehderi* but has a greater number of fine radial ribs.

Habitat. Fine muddy sand from 4–200 m.

Distribution. Senegal to Northern Angola (Fig. 28).

Material examined. **AFRICA**: Guinea, Los Islands (NMW 1955.158).

Cardiolucina rehderi (Britton, 1972)

Fig. 27 c & d

Parvilucina (Bellucina) rehderi Britton, 1972: 7–9, fig. 3.
Lucina (Parvilucina) rehderi (Britton) – Rios, 1994: 252.

Type material. Holotype, USNM 208255, L = 4.2 mm, H = 4.2 mm, T = 4.1 mm (paired valves), also 9 paratypes.

Type locality. Brazil, no further details.

Shell description. Shell small, height to 4.2 mm. Subcircular; moderately inflated, maximum tumidity on a single valve to 1.9 mm. Inequilateral, slightly extended anteriorly. Broad posterior sulcus. Posterior dorsal area slightly convex, with distinct elevation of concentric lamellae. Shallow anterior sulcus, anterior dorsal area indistinct. Lunule shallow, heart-shaped. Exterior sculpture of about 30 indistinct radial ribs most clearly visible in the interspaces between concentric lamellae, ribs separated by shallow, narrow interspaces. Concentric lamellae,14–16, prominent, thickened lamellae often appear scalloped at position of intersection with radial ribs. Hinge plate thickened. Left valve with single anterior lateral tooth; two cardinal teeth and single posterior lateral. Right valve with similar. Ligament short, extending about half distance from beak to posterior lateral tooth. Inner margin with about 20 fine crenulations. Anterior adductor muscle scar longer than wide but relatively short with pallial line joining near ventral tip. Posterior adductor muscle scar rounded. Shell colour white. A more extensive description of this species is given by Britton (1972).

Comparison with other species. This species is closely similar to *C. lamothei.*

Habitat. Unknown.

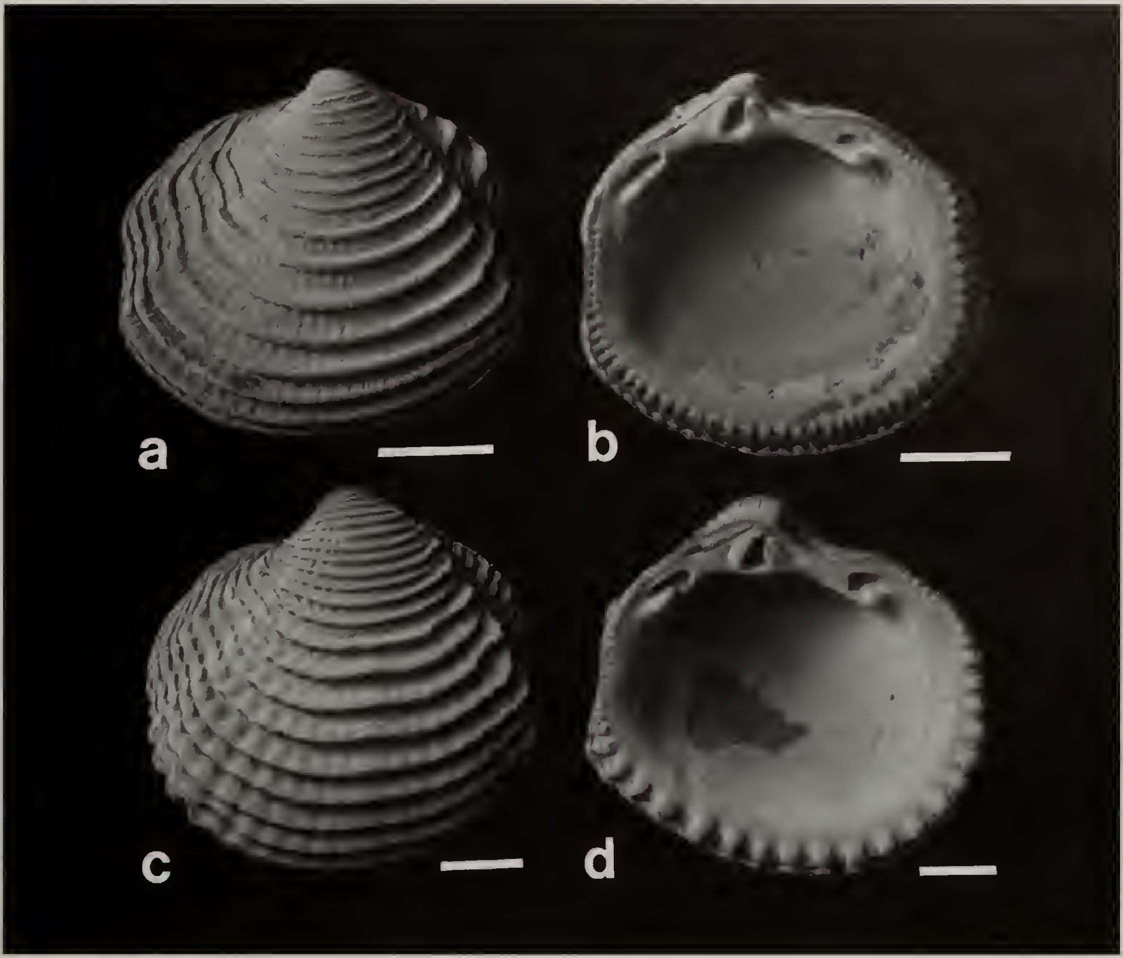

Fig. 27 *Cardiolucina lamothei* (Dautzenberg, 1913) and *C. rehderi* (Britton, 1972). a, *C. lamothei* Iles de Los, nr Conakry, Guinea (NMW 1955.158) Left valve. P35.082; b, left valve interior; c, *C. rehderi* Britton, left valve, Paratype NMNH; d, left valve interior. Scale bar a–d = 1.0mm.

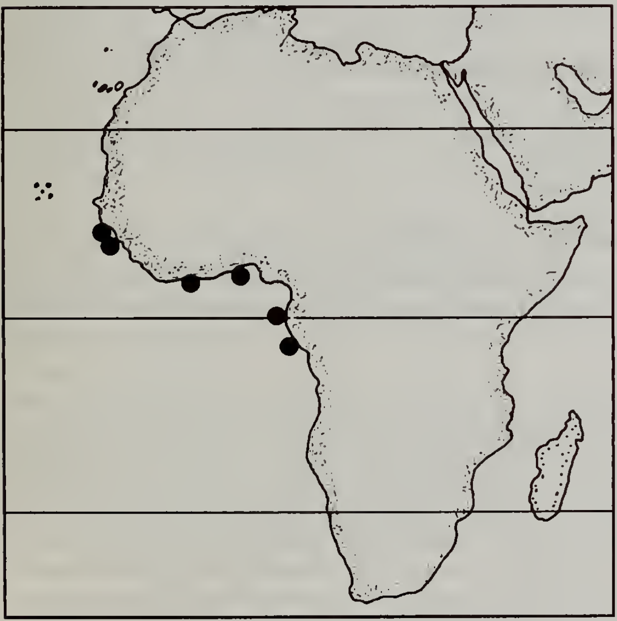

Fig. 28 Geographical distribution of *Cardiolucina lamothei* (Dautzenberg). Data from Dautzenberg (1913).

DISTRIBUTION. Known only from type material reported on by Britton (1972).

FOSSIL SPECIES OF *CARDIOLUCINA*

Apart from the description of the type species *C. agassizi,* we have not attempted a comprehensive review of the fossil record. However, the species listed below have the characters of *Cardiolucina.* Other fossil species that we do not consider to belong the genus are listed separately.

Phacoides (Parvilucina) ligatus Cossmann and Pissarro, 1904. (pages 17–18, pl. 7, figs 1–4).

Described from the Eocene (Lutetian) of Hauteville, Cotentin Peninsula, France. This small species has a thick shell and prominent concentric lamellae with fine radial ribbing similar to that of *Cardiolucina agassizi.* Chavan (1937: 207) first suggested that this species should be classified as a *Bellucina.* On the basis of the published figures, we consider that this is probably the earliest known *Cardiolucina.*

Lucina nuciformis Tate, 1887b: 144 (figured in Tate, 1886, p. 158, pl. 12 figs.10a & b).

This Miocene species from Blanche Point, Aldinga Bay, South Australia, is very similar to the Recent *Cardiolucina crassilirata* (Tate).

Linga (Bellucina) gonzalesi Shuto,1971 (pp. 30–31; Plate 1 figs 8,11,13–17; text fig. 6)

Described from the Lower Pliocene Cabatuan Formation of Panay Island, Philippines. This species is well described and illustrated. It has about eight prominent, radial ribs with a fenestrate ornament like the Recent *Cardiolucina eucosmia*, *C. pisiformis* and *C. siquijorensis*. The intersections of the radial ribs and concentric lamellae are 'strongly granulated', a feature found in none of the three Recent species.

Lucina polli Icke & Martin, 1907. (p. 250, plate 18 figs 40, 40a)

Described from the Pliocene of Nias Island, Indonesia. From the illustrations, this is a definite *Cardiolucina* species with fine radial ribbing and prominent concentric lamellae, similar in form to *C. rugosa.*

Cardiolucina agassizi var. ***regularior*** Sacco, 1904 (p. 90, pl. 20 figs. 40–42) and var. ***constricta*** Sacco,1904 (p. 90 pl. 20 fig. 43).

Without a morphological analysis of *C. agassizi* populations it is difficult to evaluate these names, but they would seem to be forms of a variable species.

SPECIES EXCLUDED FROM *CARDIOLUCINA*.

Listed under original generic assignments as published.

Phacoides (Bellucina) actinus Dall, 1903: 1385, pl. 52 fig. 3. Also Woodring (1925: 126–127; pl. 17 figs 5–8).

Described from the middle Miocene Bowden Formation of Jamaica, this species has 16–22 radial ribs and fine concentric lamellae. However, the lunule is lanceolate and the hinge different from *Cardiolucina* species. We consider that it may belong to the same clade as *Radiolucina amianta* (Dall) (see below).

Phacoides (Bellucina) amiantus Dall, 1901: 826–7, pl. 39 fig.10.

Although Dall included this Caribbean species in *Bellucina* and Bretsky (1976) used it as the basis of her diagnosis of the genus, it differs in many features from the type species of *Cardiolucina* and *Bellucina*. Britton (1972) discussed this at some length and proposed the new generic name *Radiolucina* with *P. amiantus* as the type species.

Phacoides (Bellucina) tuomeyi Dall, 1903: 1385, pl. 52 fig. 1.

Described from the late Miocene Duplin Marl of North Carolina, this species is similar to the Recent *Radiolucina amianta* (Dall).

Phacoides (Bellucina) waccamawensis Dall,1903: 1385, pl. 52 fig. 2.

Described from the Pliocene Waccamaw Formation of South Carolina, this species is closely similar to the Recent *Radiolucina amianta* (Dall) and was tentatively synonymised by Bretsky (1976).

Phacoides peritaphros Barnard, 1964: 476–477 fig. 22. Syntypes: BMNH 1964264

Although Barnard regarded this southern African species as allied to *Cardiolucina lamothei* (Dautzenberg), it lacks radial riblets, has a shallow, open lunule and is more anteriorly extended. This species is similar in many features to *Cavilinga trisulcata* (Conrad, 1841) (see Olsson and Harbison 1953, pl.7 fig. 4), the type species of the genus *Cavilinga* Chavan, 1937.

Lucina cancellaris Philippi, 1846: 21.

This is a West American twin species to the Caribbean *Radiolucina amianta.* Keen (1971, p. 121) points out that 'Dall unfortunately assigned this species and its Caribbean twin *L. amianta* (Dall, 1901), to the subgenus *Bellucina,* the type of which is an Indian Ocean form only superficially similar, and American authors have been slow to recognise the error.'

Lucina pulchella Lynge, 1909: 173, pl 3 figs. 13–15.

Lynge compared this species with *L. seminula* Gould, *L. pisum* Reeve and *L. semperiana* Issel. We examined the type material (Zoological Museum, Copenhagen) which has a different ribbing pattern from any *Cardiolucina* and lacks posterior and anterior sulci. This species may be an *Epicodakia.*

Lucina valida Smith, 1904: p.40 pl.3 fig.19.

This southern African species is very similar to and a probable senior synonym of *Phacoides peritaphros* Barnard. Syntypes: BMNH 1903.12.19.1270–4.

Cardiolucina striatula var. ***taurotrigona*** Sacco, 1901: 90, pl. 20 fig. 44–47.

Cardiolucina striatula var. ***ovatuloides*** Sacco, 1901 90 pl. 20 fig. 48.

Cardiolucina taurocrenulata Sacco, 1901: 90 pl. 20 fig. 50.

C. taurocrenulata var. ***aviculina*** Sacco, 1901: 90 pl. 20 figs 51 & 52.

Cardiolucina oligobliqua Sacco, 1901: 91 pl. 20 fig. 53.

All these taxa were described from the Miocene of Italy. They have concentric ornament only and differ in shape from the type species. In our opinion these taxa should all be excluded from *Cardiolucina*.

RELATIONSHIPS AMONGST THE SPECIES

In an attempt to establish relationships amongst the *Cardiolucina* species a preliminary phylogenetic analysis using parsimony was performed using a set of 12 shell characters. We used PAUP version 3.0, with further interpretation of characters with McClade version 3.04. Although it would have been desirable to include anatomical characters these were available for only two species. We selected as an outgroup the northeastern Pacific *Parvilucina tenuisculpta* (Carpenter, 1864), the type species of the genus *Parvilucina.* Since the

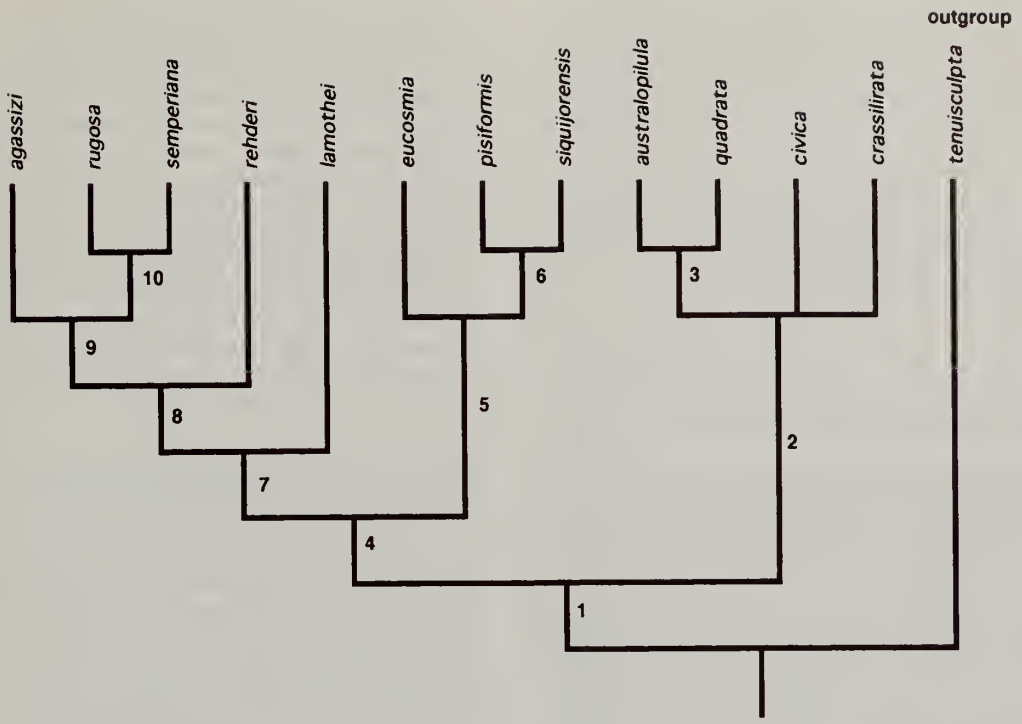

Fig. 29 Strict consensus tree of *Cardiolucina* species derived from two equally parsimonious trees. Outgroup is *Parvilucina tenuisculpta*. Character state changes at numbered internal branches. Branch 1: char. 1, state 2>1; char. 3 state 3>0; char. 6 state 2>1. Branch 2: char. 3 state 0>2; char. 8 state 0>1; char. 11 state 0>1. Branch 3: char. 11 state 1>2. Branch 4: char. 7 state 1>0. Branch 5: char. 4 state 0>1; char.5 state 0>1; char. 6 state 1>0; char. 12 state 2>0. Branch 6: char. 9 state 0>1. Branch 7: char. 1 state 1>0; char. 2 state 0>2. Branch 8: char. 12 state 2>1. Branch 9: char. 2 state 2>1. Branch 10: char.10 state 0>1.

Table 1. Characters and character state codings used in the phylogenetic analysis.

1. **Posterior sulcus.** This is an indentation in the posterior shell seen on the outer surface extending from the umbo to the shell margin. It is present in all *Cardiolucina* species, deeply incised in some (Fig. 20d), shallow in others (Fig. 2a) and weak and poorly-defined in the outgroup.
States: 0 - deep prominent;1 - shallow; 2 - weak

2. **Anterior sulcus.** This is a similar indentation at the anterior end of the shell. This is absent in some species, but where present (Fig. 20) never as prominent as the posterior sulcus.
States: 0 - absent; 1 - narrow; 2 - broad

3. **Lunule**. Many species have a heart-shaped, shallow lunule (Fig. 20c), but in *C. eucosmia* it is deeply excavated. In other species the lunule is very small and tucked under beak (Fig.2) and in the outgroup it is lanceolate.
States: 0 - shallow, heart-shaped; 1 - deeply excavated; 2 - tiny under umbo; 3 - thin lanceolate

4. **Radial ribs - number**
States: 0 - less than 20; 1 - more than 20

5. **Radial rib - shape**
Some species have prominent ribs with straight sides and separated by broad interspaces (Figs. 2,3). In others, the ribs are closer together with low rounded profiles and narrow interspaces (Figs. 7,10).
States: 0 - rounded, narrow interspaces; 1 - straight-sided broad interspaces

6. **Radial rib intersection with concentrics.**
In some species, ribs appear to cross concentric lamellae without interruption (Fig. 2d) whilst in others the ribs terminate at the intersection with major concentric lamellae (Fig. 7d). In the outgroup the radial ribs are extremely weak.
States: 0 - strong, cross concentrics ; 1 - weak, terminate at concentrics; 2 - very weak

7. **Concentric lamellae - number**
Concentric lamellae are a prominent feature of many *Cardiolucina* species.
States: 0 - less than 20; 1 - more than 20

8. **Shape of anterior cardinal tooth in left valve**
The majority of species have a triangular wedge shaped tooth (Fig. 18b) but in some species the anterior cardinal is a hook-shaped projection (Fig. 3c).
States: 0 - wedge; 1 - hooked

9. **Posterior cardinal of left valve**
Most species have a relatively thin tooth (Fig. 7c), but in *C. pisiformis* , for example, it is much thicker (Fig. 14c).
States: 0 - thin; 1 - thick

10. **Denticles on cardinal teeth**
This refers to small denticles seen at high magnification along the edges of the posterior cardinal (Fig.12d).
States: 0- absent; 1 - present

11. **Hinge buttress**
The hinge may be projected ventrally below the cardinal teeth to form a rounded buttress (Fig 3c).
States: 0 - absent; 1 - slight; 2 - prominent

12. **Margin crenulations - number**
These are seen on the internal ventral margin of shell. These were counted around the shell margin, fine beading not included.
States: 0 - coarse (n = 10-20); 1 - medium (n = 21-30); 2 - fine (31 +).

Table 2 Matrix of *Cardiolucina* species and the outgroup *Parvilucina* tenuisculpta and their character states. Character coding as in Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12
agassizi	0	1	0	1	0	1	1	0	0	0	0	1
australopilula	1	0	2	0	1	0	1	1	0	0	2	1
civica	1	0	2	1	0	1	1	1	0	0	1	2
crassilirata	1	0	2	1	0	1	1	1	0	0	1	2
eucosmia	1	1	1	0	1	0	0	0	0	1	0	0
pisiformis	1	0	0	0	1	0	0	0	1	0	0	0
quadrata	1	0	2	1	0	1	1	1	0	0	2	1
rugosa	0	1	0	1	0	1	0	0	0	1	0	1
semperiana	0	1	0	1	0	1	0	0	0	1	0	1
siquijorensis	1	0	0	0	1	0	0	0	1	?	0	0
lamothei	0	2	0	1	0	1	0	0	0	0	0	2
rehderi	0	2	0	1	0	1	0	0	0	0	0	1
P. tenuisculpta	2	0	3	1	0	2	1	0	0	0	0	2

original designation by Dall (1901), *Cardiolucina* (as *Bellucina*) has been widely listed as a subgenus of *Parvilucina* and the shells have some features in common (descriptions in Hickman 1994). Moreover, there are some similar anatomical features, *P. tenuisculpta* having a visceral lobe resembling that found in *C. semperiana* and *C. australopilula*, as well as the connection of the posterior ctenidia to the mantle and the lack of a fused inhalant aperture (Reid and Brand, 1986). The characters and their states are listed in Table 1.

The distribution of the various character states amongst the *Cardiolucina* species and the outgroup is shown in Table 2. Phylogenetic analysis using this matrix produced 2 equally parsimonious trees of 26 steps with a consistency index of 0.731 and a homoplasy index of 0.269. A strict consensus tree is shown in Fig. 29. The differences in the 2 trees resulted from the grouping of *C. civica* and *C. crassilirata* as a single clade or as a trichotomy with the *C. australopilula* /*C. quadrata* clade.

The analysis suggests that there are three distinct clades of *Cardiolucina* species (Fig. 29). Clade 1 contains *C. australopilula*, *crassilirata, civica* and *quadrata*. Apomorphies which define this clade at Branch 2 are; the tiny lunule, the hooked-shaped, anterior cardinal tooth and the hinge buttress. Clade 2, separated at Branch 4 by a single apomorphy of having less than 20 concentric lamellae, contains two major branches; that comprising the type species *C. agassizi* and the species around *C. semperiana*. (Branch 7) and another branch (Branch 5) containing *C. eucosmia*, *pisiformis* and *siquijorensis*. This latter clade is defined by four apomorphies; having less than 20 radial ribs, which are straight-sided and cross the concentric lamellae and also possess coarse marginal crenulations. The *C. agassizi – lamothei* clade is defined at Branch 7 by the prominent posterior sulcus and a broad anterior sulcus.

This hypothesis of relationships should be regarded as tentative because it is based on shell characters alone. Nevertheless, it is open to falsification by additional or alternative character sets.

GEOGRAPHICAL DISTRIBUTION

Two species, *Cardiolucina lamothei* and *C. rehderi* are found on opposite sides of the Atlantic, whilst the other nine are distributed largely within the tropical Indo-West Pacific Province. One of these, *C. semperiana*, has a wide range from the Gulf of Suez to Philippines whilst the rest have more restricted distributions within the central Indo-Pacific. Four species are endemic to Australia; *C. eucosmia*, *C. pisiformis* and *C. australopilula* to the western and northern coasts and *C. crassilirata* to the temperate southern coast. *Cardiolucina civica* occurs from Japan through Indonesia to the Andaman Islands in the west and Fiji in the east. *C. quadrata* is restricted to deeper water around the Philippines and Indonesia. Apart from *C. rehderi*, which is known from only one vague locality, the species with the most limited range is *C. siquijorenis* from Siquijor Island in the Philippines. All the species are largely tropical in distribution, except for *C. crassilirata* from southern Australia.

Table 3 Summary of shell characters in *Cardiolucina* species

Species	H	L	T	Radial ribs		Concentric lamellae		Sulcus post.	ant.	Marginal crenulae	Lunule small, under beak	heart-shaped
agassizi	7.4	7.1	2.7	c.25	faint, closely spaced	c.20	width of interspaces extremely variable	deep	narrow	28		shallow
australopilula	13.8	12.7	7.5	c.20	interspaces almost as wide as ribs	c.34–36	low, narrow	shallow	none	21	*	
civica	10.6	10.4	4.5	>30	fine, closely spaced	>25	conspicuous	shallow	none	>60	*	
crassilirata	11.0	11.3	6	>40	fine, closely spaced	>30	fine, clustered in groups of 4–6	shallow	none	31	*	
eucosmia	7.8	7.7	3.8	c.12	broad, with wide interspaces	c.13–14	low	v.deep	narrow	12		v. deep
pisiformis	4.4	4.4	2	13–17	low, widely spaced	c.20	narrow	shallow	none	13		deep
quadrata	12.9	13.6	5.3	c.25	fine,closely spaced	25–30	low, broad	shallow	none	25	*	
rugosa	3.1	3.2	1.2	>25	faint, closely spaced	c.20	prominent	deep	narrow	20		shallow
semperiana	7.7	7.5	2.7	20–30	low, closely spaced	15–24	interspaces variable in width	deep ribbed	narrow,	20–21		shallow
siquijorensis	3.5	3.5	1.3	12	broad	14–16	thin	shallow	none	12		shallow
lamothei	4	3.9	2	>40	fine, closely spaced	15–18	prominent	deep	broad	40	*	
rehderi	4.2	4.2	1.9	>30	fine, faint closely spaced	14–16	prominent	deep	broad	20	*	

H=height, max mm, L=length, max mm, T=tumidity, max mm.

The phylogenetic analysis shows that *Cardiolucina lamothei* and *C. rehderi* are closer to the *C. semperiana* clade of species than to the *C. australopilula* or *C. eucosmia* clades. This suggests that the clade containing *C. lamothei-rehderi* and *C. semperiana* had a widespread Tethyean distribution prior to the (late Miocene) closure of the connection between the Indo-Pacific and Atlantic Oceans. This is confirmed by the occurrence of *C. agassizi* in the Middle Miocene of south west Europe. The *C. australopilula* clade is restricted in distribution to the central Indo-Pacific. The Miocene species *C. nuciformis* Tate from South Australia is similar to the Recent *C. crassilirata* from the same area suggesting a long occupancy.

CONCLUSIONS

In this revision of the systematics of *Cardiolucina* we have redefined the genus and its type species and recognised eleven living species from the tropical Atlantic and Indo-W. Pacific provinces. The previous lumping of many taxa into *C. semperiana* underestimated species diversity. Table 3 provides a summary of the characters of the recognised species as an aid to identification. Anatomical characters are known for only two species, *C. australopilula* and *C. semperiana*. Comparison with other genera is difficult because of the lack of information, but *Parvilucina* has some similar characters, such as the lack of mantle fusion at the posterior inhalant area, the connection of the ctenidia to the posterior mantle and the large visceral lobe (Reid and Brand, 1986). Further work is needed to establish the distribution of these characters in other lucinid taxa.

Although the earliest *Cardiolucina* would seem to be the Eocene species *C. ligata* (Cossmann & Pissarro), the fossil record, apart from *C. agassizi* which is common in the middle Miocene of Europe, is rather scanty. The only species we can confirm are *Cardiolucina nuciformis* (Tate) from the Miocene and, from the Pliocene, *C. gonzalesi* (Shuto) and *C. polli* (Icke & Martin). This paucity of records is unsurprising because, even in Recent faunas, these small lucinids are neglected.

The problems encountered during this systematic revision reflect the current state of systematics within the family Lucinidae. Many genera are defined only by a small number of shell characters, type species of genera are often inadequately described and, moreover, their characters are often ignored by systematists. Species diversity is often greater than realised because taxa have been shoe-horned into a small number of 'well-known' names. Relationships between genera are generally unknown and rigorous phylogenetic analyses are lacking. Bretsky (1970, 1976) produced a phenetic/phylogenetic analysis of lucinid genera, with possible phylogenies for her various lineages. Unfortunately, there are problems with these phylogenies because she lumped together distinct genera and confused type species, for example, using for *Bellucina* characters of *Radiolucina amianta* instead of the type species *B. eucosmia*. Moreover, there is no anatomical or biological information available for the vast majority of species, especially those from the Indo-Pacific province. Recent studies on the chemosymbiosis of lucinids have focused on a small number of species from the Caribbean and temperate north Atlantic and Pacific (reviewed in Fisher, 1990, Le Pennec *et al.*, 1995), but biological information from these studies has yet to be integrated into lucinid systematics. Systematic and phylogenetic studies should be providing the framework to test hypotheses concerning the evolutionary history and radiation of the Lucinidae, but, at present, these are inadequate.

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